THE

PHYSIOLOGY OF MAN;

DESIGNED TO REPRESENT

THE EXISTING STATE OF PHYSIOLOGICAL SCIENCE,

AS APPLIED

TO THE FUNCTIONS OF THE HUMAN BODY.

BY

AUSTIN FLINT, JR., M.D.,

PROFESSOR OF PHYSIOLOGY AND PHYSIOLOGICAL ANATOMY IN THE BELLEVUE HOSPITAL MEDICAL COLLEGE, NEW YORK; PHYSICIAN TO THE BELLEVUE HOSPITAL; CONSULTING PHYSICIAN FOR THE CLASS OF NERVOUS DISEASES TO THE BUREAU OF MEDICAL AND SURGICAL RELIEF FOR OUT-DOOR POOR, BELLEVUE HOSPITAL; FELLOW OF THE NEW YORK ACADEMY OF MEDICINE; MEMBER OF THE MEDICAL SOCIETY OF THE COUNTY OF NEW YORK, OF THE NEW YORK SOCIETY OF NEUROLOGY AND ELECTROLOGY, ETC.

IN FIVE VOLUMES.—VOL. V.

(WITH A GENERAL INDEX TO THE FIVE VOLUMES.)

SPECIAL SENSES; GENERATION.

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PREFACE.

The present volume completes the task, begun eleven years ago, of preparing a work, intended to represent the existing state of physiological science, as applied to the functions of the human body. The kindly reception which the first four volumes have received has done much to sustain the author in an undertaking, the magnitude of which he has appreciated more and more as the work has progressed.

An elaborate treatise on the great subject of the physiology of man must be written, in this country, under certain disadvantages; and the attempt to give a fair and complete account of certain subjects has often seemed well-nigh hopeless. It soon became evident, in the progress of the work, that it is frequently unsafe to take references at second-hand, even from the best writers; and months of delay in the appearance of each volume have been due to the necessity of looking up citations, as it was desired to make reference only to original works. There are no complete libraries on physiology in this country; and, while the author has derived great assistance from the serial publications contained in the Astor Library—which he takes this occasion to acknowledge most gratefully—he has been compelled to import the greater

number of the works to which he has referred. As far as such an end could be accomplished by patient labor, the references are accurate, and given in such a way that they can be easily verified. The author has not hesitated, however, to give his own opinions upon every subject considered, even when they have been opposed to high authority.

In the preparation of this work, the author has formed his opinions, to a great extent, from the results of direct observation and experiment, as the true basis of what is positively known in physiology; and, while the earlier volumes might be modified by the addition of new facts, they contain comparatively little that has been disproved by recent investigations. Experimental observations have been studied and criticised from a practical point of view; and, in this, the author's training as an experimentalist and a public teacher for more than fifteen years has given him a certain degree of confidence. It is the practical physiologist who is best qualified to judge of the correctness of the results of physiological experiments and of the accuracy of methods of investigation; and the author has learned, from his own attempts at original observation, to estimate the difficulties of direct research and to appreciate the inaccuracies into which careless, inexperienced, or over-enthusiastic workers are liable to fall.

As regards certain new views enunciated in the first four volumes, the author has found no reason to modify his opinions. In the first volume, under the head of respiration, he stated, as the result of numerous experiments, that the *besoin de respirer*, or sense of want of air, the impression which gives rise to the first inspiratory effort in the newly-born and which excites the reflex acts in normal respiration, is refer-

able, not to the lungs, but to the general system, and is due to want of oxygen and not to the stimulation of carbonic acid. This view, originally published in 1861,[1] has been confirmed by farther study and observation.

In 1862, the author published an account of a new excretory function of the liver, consisting in the separation of cholesterine from the blood, and its discharge in the fæces, in the form of stercorine.[2] This discovery the author regarded as of great importance, pathologically as well as physiologically, as it gave an idea of the pathology of certain diseases of the liver in which cholesterine is retained in the blood, constituting the condition described by the author under the name of cholesteræmia. The fact of such a retention of cholesterine was demonstrated in many cases in the human subject; but the views of the author have lately received complete confirmation by the experiments of Dr. Koloman Müller, who produced cholesteræmia, with all the symptoms of "grave icterus," by injecting cholesterine into the veins of dogs.[3] It seems to the author that his views upon this point must now take a permanent place in science.

In the third volume, the author adheres to the view that sugar is produced by the liver during life, and reconciles the discordant observations upon this point, by demonstrating that the sugar thus produced is washed out by the blood as fast as it is formed, and may not be found in the liver itself, if this organ be examined a few seconds after death.[4] This view has been adopted by many writers, as settling the controversy with regard to the function of glycogenesis.

[1] *American Journal of the Medical Sciences*, Philadelphia, October, 1861.

[2] Ibid., October, 1862.

[3] *Archiv für experimentelle Pathologie und Pharmakologie*, Leipzig, 1873, Bd. I., Drittes Heft.

[4] *New York Medical Journal*, January, 1869.

In 1871, the author published an elaborate series of investigations on the physiological effects of severe and protracted muscular exercise, with special reference to its influence upon the excretion of nitrogen.[1] If the simple facts resulting from these investigations be accepted as true, they fully confirm the view enunciated in the third volume—which is directly opposed to the opinions of many recent observers—that muscular exercise largely increases the elimination of urea.

In the fifth and last volume, an attempt has been made to give a clear account of the physiology of the special senses and generation, a most difficult and delicate undertaking. With regard to the chapters on vision, the author desires to express his acknowledgments, for most valuable aid, to his colleague, Professor H. D. Noyes, who carefully overlooked this portion of the work and made many important corrections and suggestions. If this section be found fully up to the present day in ophthalmology, it is largely due to the assistance rendered by Professor Noyes.

Finally, as regards the last, as well as the former volumes, the author can only say that he has spared neither time nor labor in their preparation; and the imperfections in their execution have been due to deficiency in ability and opportunity. He indulges the hope, however, that he has written a book which may assist his fellow-workers, and interest, not only the student and practitioner of medicine, but some others who desire to keep pace with the progress of Natural Science.

[1] *New York Medical Journal*, June, 1871.

NEW YORK, *May*, 1874.

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PHYSIOLOGY OF MAN.

CHAPTER I.

SPECIAL SENSES—TOUCH, ETC.

General characters of the special senses—Muscular sense (so called)—Appreciation of weight—Sense of touch—Variations in tactile sensibility in different parts—Table of variations measured by the æsthesiometer—Connection between the variations in tactile sensibility and the distribution of the tactile corpuscles—Titillation—Appreciation of temperature—Venereal sense.

Our study of the nervous system, in the volume devoted to that subject, has involved simply motion and what is known as general sensibility; and almost all our positive knowledge of these properties has been derived from experiments upon the inferior animals. As regards sensation, the experiments have referred to impressions recognized as painful; and we have seen that these are conveyed to the centres by nerve-filaments, anatomically as well as physiologically distinct from those which convey to the contractile parts the stimulus that gives rise to motion. As far as we have studied the sensory nerves, we have alluded to simple impressions only; but it is evident that the filaments of peripheral distribution of these nerves are capable of receiving a variety of impressions, by which we determine, to a certain extent, the form, size, character of surface, density, and temperature of objects. We also have a general appreciation of heat and cold; a sense of resistance, which gives an idea of weight; and, finally, there are nerves of peculiar properties, termi-

nating in organs calculated to receive the impressions of smell, sight, hearing, and taste.

The senses of olfaction, vision, audition, and gustation belong to peculiar organs, provided with nerves of special properties, which are not usually endowed with general sensibility. These nerves have been omitted in our general study of the nervous system; and the accessory organs to which they are distributed are so important and intricate in their structure as to demand extended description.

The senses of touch, titillation, temperature, and pain are all conveyed to the nerve-centres by what we have described as ordinary sensory nerves; the touch being perfected in certain parts by peculiar arrangements of the terminal nerve-fibres. Though it be possible that each one of these impressions may be transmitted by special and distinct fibres, this has not yet approached a positive demonstration. The so-called muscular sense, by which we appreciate weight, resistance, etc., undoubtedly depends, to a great extent, if not entirely, upon the muscular nerves. In our study of the passage of the nerve-fibres to the encephalon through the spinal cord, it has been seen that most of the motor fibres decussate in mass at the medulla oblongata, and that the sensory fibres decussate throughout the entire length of the spinal axis. This important anatomical and physiological fact enables us to separate pretty clearly the muscular sense, so called, from the various modifications of general sensibility just mentioned. Dr. Brown-Séquard has observed, in a number of cases of disease of the cord, etc., in the human subject, that the conductors of the impressions of touch, titillation, pain, and temperature decussate in the cord, while the conductors of the "muscular sense"—if such a sense exist—decussate at the medulla oblongata.[1]

[1] Brown-Séquard, *Recherches sur la transmission des impressions de tact, de chatouillement, de douleur, de température, et de contraction (sens musculaire) dans la moelle épinère.—Journal de la physiologie*, Paris, 1863, tome vi., p. 125.

Muscular Sense (so called).

It is difficult to define exactly what is meant by the term muscular sense, as it is used by many physiologists. In all probability, the sense which enables us to appreciate the resistance, immobility, and elasticity of substances that are grasped, on which we tread, or which, by their weight, are opposed to the exertion of muscular power,[1] is immensely modified by education and habit. Still, it is undoubtedly true that the general sensibility regulates the action of muscles to a very great extent. If, for example, the lower extremities be paralyzed as regards sensation, the muscular power remaining intact, the person affected cannot walk, unless he be able to see the ground. In these cases, the individual often falls when blindfolded, for the simple reason that his limbs have lost the sense of contact with the ground, which is nothing more nor less than loss of general sensibility. Many curious examples of this kind are to be found in works upon diseases of the nervous system. One of the most striking is a case communicated to Sir Charles Bell by Dr. Ley. The patient was afflicted with partial loss of sensibility upon one side of the body, "without, however, any corresponding diminution of power in the muscles of volition, so that she could hold her child in the arm of that side so long as her attention was directed to it; but, if surrounding objects withdrew her from the notice of the state of her arm, the flexors gradually relaxed, and the child was in hazard of falling."[2] This is precisely like the phenomena ordinarily described under the head of locomotor ataxia. In this disorder, there is disease of the posterior columns of the spinal cord, with progressive loss of general sensibility, the muscular power, in some instances, being intact. Patients affected in this way cannot walk or stand unless they be able to supply the sense of contact by the sight. One of the most

[1] See vol. iii., Movements, p. 460. We have here treated of the sensibility of the muscles in its relations to movements.

[2] Bell, *The Nervous System of the Human Body*, London, 1844, p. 245.

characteristic phenomena is inability to stand when blindfolded; although, with the aid of the sight, the muscles can be made by the will to act with great power.

Without entering into a full discussion of the various arguments used for and against the existence of a special "muscular sense," it is sufficient to state that, in those cases in which general sensibility is lost or seriously impaired, the brain has no exact appreciation of the action of the muscles, except as regards the sense of fatigue. This question is of great importance in connection with the pathology of the nervous system; and it seems that the weight of evidence is decidedly in favor of the view, that there is no distinct perception of muscular action, aside from general sensibility, that can properly be called a muscular sense.

Habit and education enable us to appreciate with great nicety differences in weight; but this is chiefly due to the sense of resistance to muscular effort, and has little dependence upon the sense of touch. In the elaborate and classical experiments of Weber, this point was very strikingly illustrated. The observations of this physiologist upon the sense of touch and general sensibility were very varied and extensive; and, among the most important of the results with regard to the appreciation of pressure and weight, are the following:[1]

In general, those parts which are most sensitive to the impressions of touch, as the fingers, enable us to appreciate differences in pressure and weight with the greatest accuracy. The sense of simple pressure, unaided by the estimation of weight by muscular effort, is generally more acute upon the left side, probably because the integument of the left hand is thinner than that of the right hand. Differences in weight can be accurately distinguished, when they amount to only one-sixteenth, by employing muscular effort in lifting, as well as the sense of pressure; but the sense of pressure alone

[1] Weber, *Drucksinn*, in Wagner, *Handwörterbuch der Physiologie*, Braunschweig, 1846, Bd. iii., Zweite Abtheilung, S. 548, *et seq.*

enables us to appreciate a difference of not less than one-eighth. When weights are tested by lifting with the hand, the appreciation of slight differences is more delicate when the weights are successively tested with the same hand than when two weights are placed, one on either hand. When the interval between the two trials amounts to more than forty seconds, slight differences in weight, for example, the difference between fourteen and a half and fifteen ounces, cannot be accurately appreciated. In such trials, it is necessary to have the metals used of the same temperature, for cold metals seem heavier than warm.

These observations formularized some of the facts, sufficiently evident to every one, relating to the appreciation of slight differences in weight. It is well known that experts acquire, in this regard, wonderful delicacy and accuracy. Those who are in the daily habit of handling coins not only count with astonishing rapidity, but are able to detect and throw out a light piece instantly and with unerring certainty.

Sense of Touch.

We have already considered, in the volume on the nervous system, the modes of termination of the sensory nerves;[1] and, in many instances, it is possible to explain, by the anatomical characters of the nerves, the great differences that have been observed in the delicacy of the tactile sensibility in different parts; differences which are exceedingly important, pathologically as well as physiologically, and which have been studied by Weber, Valentin, and others, with great minuteness.

Variations in the Tactile Sensibility in different Parts.—In certain parts of the cutaneous surface, the general sensibility is much more acute than in others. For example, a sharp blow upon the face is more painful than a similar injury to other parts; and the eye, as is well known, is most

[1] See vol. iv., Nervous System, p. 36, *et seq.*

exquisitely sensitive. The appreciation of temperature also varies in different parts, this probably depending to a great extent upon habitual exposure. Some parts, as the soles of the feet or the axilla, are peculiarly sensitive to titillation. The sense of touch, however, by which we appreciate the size, form, character of the surface, consistence, etc., of objects, is developed to a greater degree in some parts than in others; a fact which can be very readily explained, in some instances, by the anatomical arrangements of the peripheral sensory nerves. When we wish to ascertain those properties of objects revealed by the sense of touch, we generally employ the fingers. This sense is capable of education, and is almost always extraordinarily developed in persons who are deprived of other special senses, as sight or hearing. The blind learn to recognize individuals by feeling of the face. A remarkable instance of this is quoted in works on physiology, of the blind sculptor, Giovanni Gonelli, who was said to model the most striking likenesses entirely by the sense of touch. Other instances of this kind are on record. The blind have been known to become proficients in conchology and botany, guided simply by the sense of touch. It is related of a blind botanist, that he was able to distinguish ordinary plants by the fingers and by the tip of the tongue. It is well known that the blind learn to read with perfect facility, by passing the fingers over raised letters but little larger than the letters in an ordinary folio Bible.[1] Rudolphi cites the remarkable faculty acquired by Baczko, of distinguishing the colors of fabrics by the sense of touch alone.[2]

An exceedingly ingenious and accurate method of determining the relative delicacy of the tactile sensibility of different portions of the cutaneous surface was devised a number of years ago (1829) by E. H. Weber, whose researches on this subject, which have been repeatedly confirmed by other

[1] CARPENTER, *Cyclopædia of Anatomy and Physiology*, London, 1849–1852, vol. iv., part ii., p. 1179, *et seq.*, Article, *Touch.*

[2] RUDOLPHI, *Grundiss der Physiologie*, Berlin, 1823, Bd. ii., S. 85.

observers, are still the most careful and reliable on record.[1] This method consists in the application to the skin of two fine, but blunt points, separated from each other by a known distance. The individual experimented upon should be blindfolded, and the points applied to the skin simultaneously. By carefully adjusting the distance between the points, a limit will be reached where the two impressions upon the surface are appreciated as one; *i. e.*, by gradually approximating them, the subject will suddenly feel both points as one, when, an instant before, with the points a little farther removed from each other, he distinctly felt two impressions. This gives a very accurate measure of the delicacy of the tactile, as distinguished from the general sensibility of different parts, and it has lately been found a most important guide in the investigation of diseases of the nervous system attended with partial anæsthesia of the surface. Of course, the instrument used may be very simple (a pair of ordinary dividers will answer), but it is convenient to have some ready means of ascertaining the distances between the points. An instrument, consisting simply of a pair of dividers, with a graduated bar giving a measure of the separation of the points, is the best, as it combines simplicity, convenience of use, and portability.[2] This instrument is called the æsthesiometer.

The experiments of Weber were made upon his own person, and of course do not show the variations that may occur in different individuals in health, a point of considerable importance in estimating the extent of anæsthesia in disease. His observations also showed some slight variations with the direction of the line of the two points, but these are not important. Valentin repeated the experiments of Weber, and, in addition, took the maximum, minimum, and mean, in

[1] WEBER, *Ortsinn in der Haut*, in WAGNER, *Handwörterbuch der Physiologie*, Braunschweig, 1846, Bd. iii., Zweite Abtheilung, S. 524, *et seq.*

[2] The instrument described above is made by Messrs. G. Tiemann & Co., of New York.

six persons.[1] Aside from these observations, the repetition of Weber's experiments has done little more than confirm the original facts.[2] The table upon the next page, taken from the article in the *Cyclopædia of Anatomy and Physiology*, which we have already quoted, gives the results obtained by Weber and by Valentin.[3]

If we note the distribution of the tactile corpuscles in connection with this table, it will be seen that the sense of touch is most acute in those situations in which the corpuscles are most abundant. In the space of about one-fiftieth of a square inch on the palmar surface of the third phalanx of the index-finger, Meissner counted the greatest number of corpuscles; viz., one hundred and eight.[4] In this situation, the tactile sensibility is more acute than in any other part of the skin, the mean distance indicated by the æsthesiometer being 0·603 of a line. In the same space on the second phalanx, forty corpuscles were counted, the æsthesiometer marking 1·558 line, this part ranking next in tactile sensibility after the red surface of the lips.

We can readily understand how the hard tactile corpuscles, embedded in the amorphous substance of the cutaneous papillæ, might increase the power of appreciation of delicate impressions.

As regards the general cutaneous surface in which no tactile corpuscles have been demonstrated, it is not easy to connect the variations in the tactile sensibility with the nervous distribution, as we know little or nothing of the comparative richness of the terminal nervous filaments in these situations.

[1] VALENTIN, *Physiologie des Menschen*, Braunschweig, 1844, Bd. ii., S. 558.

[2] The above remark applies to a recent publication by Vierordt, on the causes of the different development of the sense of locality of the skin (*Archiv für die gesammte Physiologie*, Bonn, 1870, Bd. ii., S. 297). In this article, it is proposed to show that the tactile sensibility of the skin is acute in proportion to the mobility of the parts which it covers.

[3] CARPENTER, *op. cit.*, vol. iv., part ii., p. 1169.

[4] See vol. iv., Nervous System, p. 40.

Table of Variations in the Tactile Sensibility of Different Portions of the Skin (WEBER and VALENTIN).

The tactile sensibility is measured by the greatest distance between two points at which they convey a single impression when applied simultaneously. The measurements are given in lines ($\frac{1}{12}$ of an inch).

PART OF SURFACE.	WEBER.	VALENTIN.				
		Max.	Min.	Mean.	Relative acuteness.	Relative obtuseness.
Tip of the tongue	0·50	0·50	0·40	0·468	1·000	1·000
Palmar surface of third phalanx of forefinger	1·00	1·00	0·50	0·608	0·802	1·248
do. do. middle finger	....	1·00	0·87	0·706	0·655	1·461
do. do. ring-finger	....	1·00	0·60	0·728	0·669	1·496
do. do. thumb	....	1·00	0·50	0·725	0·667	1·500
do. do. little finger	....	1·00	0·50	0·788	0·659	1·517
Red surface of under lip	2·00	2·00	0·50	1·500	0·322	8·130
do. upper lip	....	2·00	0·50	1·520	0·318	8·145
Palmar surface of second phalanges of fingers	2·00	2·00	1·25	1·558	0·310	8·223
do. first do.	....	1·75	1·50	1·650	0·298	8·414
Middle of the dorsum of the tongue	4·00	4·00	1·50	1·916	0·252	8·964
Dorsal surface of the third phalanges of fingers	8·00	8·00	1·75	2·125	0·227	4·397
Portion of the lips not red	4·00	4·00	1·50	2·208	0·219	4·568
Tip of the nose	8·00	8·00	0·50	2·250	0·215	4·655
Edge of the tongue an inch from the tip	....	4·00	1·50	2·478	0·195	5·127
Lateral surface of the dorsum of the tongue	....	4·00	1·50	2·500	0·198	5·172
Palmar surface of the metacarpus	8·00	8·00	1·75	2·625	0·184	5·431
End of the great-toe	5·00	5·00	8·00	8·250	0·149	6·724
Metacarpal joint of the thumb	4·00	4·50	2·00	8·333	0·145	6·896
External surface of the eyelids	5·00	5·00	2·50	8·888	0·126	7·980
Palm of the hand	5·00	5·00	8·00	8·888	0·126	7·980
Dorsal surface of second phalanx of thumb	5·00	5·50	2·75	8·598	0·124	8·054
do. do. forefinger	....	5·50	2·75	8·898	0·124	8·054
do. do. middle finger	....	5·50	2·75	8·900	0·124	8·069
do. do. little finger	....	5·50	2·50	8·948	0·122	8·158
do. do. ring-finger	....	5·50	2·75	8·971	0·121	8·216
Centre of the hard palate	6·00	6·00	2·00	4·042	0·120	8·368
Mucous membrane of lips close to the gum	9·00	9·00	2·00	4·125	0·117	8·585
Skin of cheek over buccinator	5·00	5·00	8·25	4·541	0·106	9·395
do. over anterior part of malar bone	7·00	7·00	8·00	4·620	0·105	9·559
Dorsal surface of first phalanges of fingers	7·00	7·00	4·00	4·917	0·098	10·178
Prepuce	....	6·00	4·00	5·100	0·095	10·552
Dorsal surface of heads of metacarpal bones	8·00	8·00	8·25	5·250	0·092	10·862
Skin of cheek over posterior part of malar bone	10·00	10·00	8·00	5·286	0·091	10·936
Plantar surface of metacarpal bone of great toe	....	7·00	5·00	5·875	0·082	12·155
Lower part of forehead	10·00	10·00	4·00	6·000	0·081	12·414
Back of the hand	14·00	14·00	8·50	6·966	0·069	14·412
Lower part of hairy scalp in occipital region	12·00	12·00	6·00	8·292	0·058	17·156
Surface of the throat beneath lower jaw	15·00	15·00	8·00	8·292	0·058	17·156
Back of the heel	10·00	10·00	8·00	9·000	0·054	18·621
Pubes	....	14·00	8·00	9·200	0·052	19·035
Crown of the head	15·00	15·00	5·50	9·583	0·050	19·827
Patella and surrounding part of thigh	16·00	16·00	6·00	10·208	0·047	21·120
Areola around nipple	....	20·00	9·50	12·066	0·040	24·964
Dorsum of foot near the toes	18·00	18·00	7·50	12·525	0·039	25·914
Axilla	....	14·00	12·00	13·000	0·037	26·897
Upper and lower extremities of forearm	18·00	18·00	7·00	13·292	0·036	27·501
Back of the neck near the occiput	24·00	24·00	8·00	13·292	0·036	27·501
Upper and lower extremities of leg	18·00	18·00	9·00	13·708	0·035	28·361
Penis	18·00	18·00	10·00	13·850	0·034	28·655
Acromion and upper part of arm	18·00	18·00	6·00	13·866	0·034	28·688
Sacral region	18·00	18·00	7·50	14·958	0·032	30·948
Sternum	20·00	20·00	8·00	15·875	0·030	32·845
Gluteal region and neighboring part of thigh	18·00	18·00	10·50	16·625	0·029	34·397
Middle of forearm where its circumference is greatest	30·00	30·00	8·75	17·083	0·028	35·344
Middle of thigh do.	30·00	30·00	9·00	17·633	0·027	36·482
Middle of cervical vertebræ	30·00	30·00	7·00	18·542	0·026	38·362
Five upper dorsal vertebræ	24·00	24·00	11·00	19·000	0·025	39·310
Lower part of thorax and over lumbar vertebræ	24·00	24·00	11·50	19·912	0·022	44·758
Middle of dorsal vertebræ	30·00	30·00	11·00	24·208	0·020	50·086

Titillation.—The sensation experienced when certain parts of the general surface are subjected to titillation cannot easily be described, though it is sufficiently familiar. This sensation is simply due to delicate impressions made in unusual situations, and is remarkable chiefly on account of the reflex movements which it occasions. If the soles of the feet be tickled, it is almost impossible to avoid movements of the limbs. These are not due entirely to the peculiar sensation appreciated by the brain, for the same stimulus, in persons suffering from complete paralysis of sensation and voluntary motion of the lower extremities, may produce even violent action of the paralyzed muscles. These phenomena have been fully described in connection with reflex action. There are no facts, experimental or clinical, showing that the peculiar sense of titillation is conveyed to the encephalon by nerve-fibres other than those of general sensibility. The peculiar nature of the sensation is due to the unusual character of the impression, and does not involve the action of special nerve-fibres as conductors.

Appreciation of Temperature.—It is not known that the sense of temperature, either of the surrounding medium or of bodies applied to different parts of the skin, is appreciated through any other nerves than those of general sensibility, or that there is any special arrangement of the terminations of certain of the nerves connected with this sense. As regards the general temperature, the sense is relative, and is much modified by habit. This statement needs no explanation. As is well known, what is cold for an inhabitant of the torrid zone would be warm for one accustomed to an excessively cold climate.[1] Habitual exposure also modifies the sense of temperature. Many persons not in the habit of dressing warmly suffer but little in extremely cold weather. Those

[1] We do not take into account, in this connection, the remarkable fact, that inhabitants of warm climates, for a certain time, may bear long-continued exposure to cold better than those accustomed to a lower temperature.

who habitually expose the hands, or even the feet, to cold, render these parts quite insensible to temperature; and the same is true for those who often expose the hands, face, etc., to heat.

The variations in the sensibility of different parts of the surface to temperature depend, as we have just indicated, to a great extent, upon habit, exposure, etc., but also upon special properties of the parts themselves. The differences, however, are not so marked as to be of any great importance, and the experiments made upon this point are simply curious. It is remarkable, however, to note the exquisite sensibility to variations in temperature sometimes presented by those who are deprived of other senses. The example is quoted by Dunglison, of Dr. Saunderson, formerly Professor of Mathematics at Cambridge, England, who, "when some of his pupils were engaged in taking the altitude of the sun, could tell, by the slight modification in the temperature of the air, when very light clouds were passing over the sun's disk."[1]

The experiments of Weber show conclusively that the skin is the main organ for the appreciation of temperature, if we except the mouth, palate, vagina, and rectum, by which the difference between warm and cold substances is readily distinguished. In several instances in which large portions of the skin were destroyed by burns and other injuries, experiments have been made by applying spatulas of different temperatures. At one time a spatula plunged in water at from 48° to 55° Fahr. was applied to a denuded surface, and again, a spatula at from 113° to 122° Fahr. When the patient was requested to tell which was the warmer, the answers were as frequently incorrect as they were correct; but the discrimination was easy and certain when the applications were made to the surrounding healthy skin. When applications at a higher temperature were made to the denuded part, the patient suffered only pain.[2]

[1] DUNGLISON, *Human Physiology*, Philadelphia, 1856, vol. i., p. 697.

[2] WEBER, *Der Tastsinn und das Gemeingefühl*, in WAGNER, *Handwörterbuch der Physiologie*, Braunschweig, 1846, Bd. iii., Zweite Abtheilung, S. 513.

The venereal sense, which we shall not attempt to describe, is unlike any other sensation, and is general, as well as referable to the organs of generation. In this connection, however, it is interesting to note that the tactile sensibility of the palmar surface of the third phalanx of the fingers, measured by the æsthesiometer, compared with the sensibility of the penis, is as 0·802 to 0·034, or between twenty-three and twenty-four times greater.

CHAPTER II.

OLFACTORY NERVES—OLFACTION.

Nasal fossæ—Schneiderian and olfactory membrane—Physiological anatomy of the olfactory nerves—Olfactory bulbs—Olfactory cells and terminations of the olfactory nerve-fibres—Properties and functions of the olfactory nerves—Cases of anosmia in the human subject—Mechanism of olfaction—Relations of olfaction to the sense of taste—Reflex acts through the olfactory nerves.

THE nerves directly connected with the senses of olfaction, vision, and audition, are but slightly, if at all, endowed with general sensibility. As regards the olfactory nerves, the parts to which they are distributed are so fully supplied with branches from the fifth, that it is difficult to determine the fact of their sensibility or insensibility to ordinary impressions. These nerves, however, are distributed to the mucous membrane of that portion of the nasal cavity endowed with the special sense of smell. Before taking up their physiological anatomy, we shall describe briefly the parts to which the olfactory sense is probably confined.

Nasal Fossæ.—The two irregularly-shaped cavities in the middle of the face, opening in front by the anterior nares and connected with the pharynx by the posterior nares, are called the nasal fossæ. The membrane lining these cavities is generally called the Schneiderian mucous membrane,[1] and sometimes, particularly by the French, the pituitary mem-

[1] Some authors distinguish the olfactory membrane, lining the upper part of the nasal fossæ, from the rest, calling the membrane lining those parts not endowed with the sense of smell, the Schneiderian membrane. (KÖLLIKER, *Handbuch der Gewebelehre*, Leipzig, 1867, S. 741.) Most writers, however, apply the term Schneiderian membrane to the general lining membrane of the fossæ.

brane. This membrane is closely adherent to the fibrous coverings of the bones and cartilages by which the nasal fossæ are bounded, and is thickest over the turbinated bones. It is continuous with the membrane lining the pharynx, the nasal duct and lachrymal canals, the Eustachian tube, the frontal, ethmoidal, and sphenoidal sinuses, and the antrum. There are openings leading from the nasal fossæ to all of these cavities.

The essential organ of olfaction is the mucous membrane lining the upper half of the nasal fossæ. Not only has it been shown anatomically that this part only of the membrane receives the terminal filaments of the olfactory nerves, but physiological experiments have demonstrated that it is the only part capable of receiving odorous impressions. If a tube be introduced into the nostril, placed horizontally over an odorous substance so that the emanations cannot penetrate its caliber, no odor is perceived, though the parts below the end of the tube might receive the emanations; but, if the tube be now directed toward the odorous substance, so that the emanations can penetrate to the upper portion of the nares, the odor is immediately appreciated.[1]

That portion of the lining of the nasal fossæ properly called the olfactory membrane extends from the cribriform plate of the ethmoid bone downward a little less than an inch. It is exceedingly soft and friable, very vascular, thicker than the rest of the Schneiderian membrane, and, in man, has rather a yellowish color. It is covered by long, delicate, columnar cells, nucleated, each one provided with from three to eight ciliary processes, their movement being from before backward.[2] The existence of cilia in this situation has been denied by some observers.[3] The mucous glands of the olfactory membrane are numerous, long, and racemose.[4] They

[1] Longet, *Traité de physiologie*, Paris, 1869, tome iii., p. 45.
[2] Sappey, *Traité d'anatomie*, Paris, 1871, tome iii., p. 654.
[3] Kölliker, *Handbuch der Gewebelehre*, Leipzig, 1867, S. 741.
[4] Sappey, *loc. cit.*

secrete a fluid which keeps the surface moist, a condition essential to the accurate perception of odorous impressions.

Physiological Anatomy of the Olfactory Nerves.—The apparent origin of the olfactory nerve is by three roots, from the inferior and internal portion of the anterior lobe of the cerebrum, in front of the anterior perforated space. The three roots are an external and an internal white root, and a middle root composed of gray matter. The external white root is long and delicate, passing outward across the fissure of Sylvius to the middle lobe of the cerebrum. The internal white root is thicker and shorter than the external root, and arises from the most posterior portion of the anterior lobe. The middle, or gray root, arises from a little eminence of gray matter situated on the posterior and inner portion of the inferior surface of the anterior lobe.

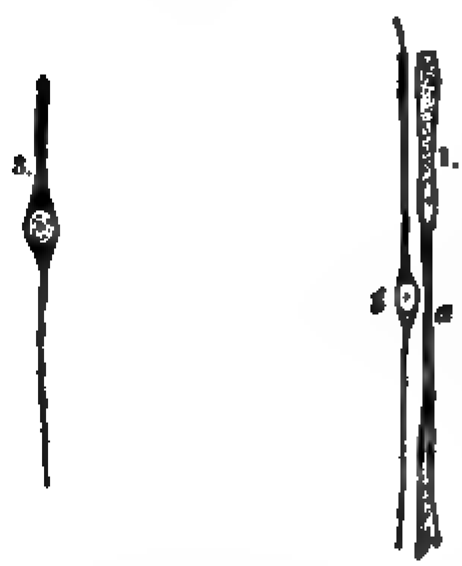
The deep origin of these three roots is still a matter of discussion. The external root is stated by various anatomists to originate from the corpus striatum, the optic thalamus, the anterior commissure, and the island of Reil; but researches upon this point have been by no means satisfactory. The same uncertainty exists with regard to the deep origin of the internal white root and the gray root.

The three roots of the olfactory converge to form a single nervous cord at the inner boundary of the fissure of Sylvius. This passes forward and slightly inward in a deep groove between two convolutions on the under surface of the anterior lobe, covered by the arachnoid membrane, to the ethmoid bone. This portion of the nerve is exceedingly soft and friable. It is composed of both white and gray matter, the proportions being about two-thirds of the former to one-third of the latter. The gray substance, derived from the gray root, is situated at the upper portion of the nerve, the white substance occupying the inferior and lateral portions.

By the side of the crista galli of the ethmoid bone, the nerve-trunk expands into an oblong ganglion, called the olfac-

tory bulb. This is grayish in color, excessively soft, and contains the ordinary ganglionic elements. From the olfactory bulb, from fifteen to eighteen nervous filaments are given off, which pass through the foramina in the cribriform plate of the ethmoid. These filaments are composed entirely of nerve-fibres and are quite resisting, owing to fibrous elements prolonged from the dura mater. It is strictly proper, perhaps, to regard these as the true olfactory nerves, the cord leading from the olfactory bulb to the cerebrum being more properly a commissure. Having passed through the cribriform plate, the olfactory nerves are distributed to the olfactory membrane in three groups; an inner group, distributed to the mucous membrane of the upper third of the septum; a middle group, to the upper portion of the nasal fossæ; and an outer group, to the mucous membrane covering the superior and middle turbinated bones and a portion of the ethmoid.

FIG. 1.



1. From the frog.—*a*, epithelial cells of the olfactory region; *b*, olfactory cells. 2. Small branch of the olfactory nerve of the frog, separating at one end into a brush of varicose fibrils. 3. Olfactory cell of the sheep. Magnified 350 diameters. (KÖLLIKER, *Handbuch der Gewebelehre*, Leipzig, 1867, S. 743.)

The mode of termination of the olfactory nerves differs from that of the ordinary sensory nerves, and is peculiar and characteristic, as it is in the other organs of special sense. According to the observations of Eckhard and Schultze, confirmed by Kölliker,[1] the olfactory mucous membrane contains peculiar terminal nerve-cells, called the olfactory cells, which are placed between the cells of epithelium. These are long, delicate, spindle-shaped structures, varicose, each one containing a clear, round nucleus. The appearance of these, which are considered as the true olfactory organs, is represented in Fig.

[1] KÖLLIKER, *Handbuch der Gewebelehre*, Leipzig, 1867, S. 743.

1. In the frog, there is a fine, hair-like process projecting from each cell beyond the mucous membrane, which has not been observed in man or the mammalia. The great delicacy of the structures entering into the composition of the olfactory membrane renders the investigation of the termination of its nervous filaments exceedingly difficult.

Properties and Functions of the Olfactory Nerves.—It is almost certain that the olfactory nerves possess none of the general properties of the ordinary nerves belonging to the cerebro-spinal system, but that they are endowed with the special sense of smell alone. As far as we know, no one has exposed and operated upon the filaments coming from the olfactory bulbs and distributed to the pituitary membrane in living animals; but the experiments of Magendie upon the nerves behind the olfactory bulbs show that they are entirely insensible to ordinary impressions. Magendie, it is true, denied that the olfactory nerves had any connection with the sense of smell, an opinion entirely untenable and contradicted by numerous experiments and pathological observations; but his experiments showing the insensibility of the nerves to ordinary impressions were entirely conclusive.[1] Attempts have been made to demonstrate, in the human subject, the special properties of these nerves, by passing a galvanic current through the nostrils; but the situation of the nerves is such that these observations are of necessity indefinite and unsatisfactory.[2] On one or two occasions, in witnessing surgical operations upon the upper part of the nasal fossæ, we have been struck with the exceedingly dull sensibility of its mucous membrane.

The question as to whether or not the olfactory nerves endow the membrane of the nasal fossæ with the sense of smell hardly demands discussion at the present day. It must

[1] MAGENDIE, *Le nerf olfactif est-il l'organe de l'odorat? Expériences sur cette question.—Journal de physiologie*, Paris, 1824, tome iv., p. 169.

[2] MEYER, *Electricity in its Relations to Practical Medicine*, New York, 1869, p. 73.

be evident to any one who reads the experiments of Magendie, in which he attempted to show that the sense of smell was retained after division of these nerves, that he confused the general sensibility of the parts with the peculiar impressions of odors; and the cases, especially the one reported by Bernard, in the human subject, in which it was supposed that the olfactory sense existed, notwithstanding congenital absence of the olfactory nerves and bulbs,[1] are by no means satisfactory, in view of the numerous instances in which precisely the opposite has been observed.

The more recent experiments upon animals are entirely conclusive as regards the effects of division of the olfactory nerves. Eschricht published, in 1826, a curious experiment in contradiction to one of the observations of Magendie. He extirpated, in a toad, the cerebral hemispheres and the olfactory bulb and nerves. Upon applying liquor ammoniæ to the nostrils of the animal, it drew back, moved the head and rubbed its nose with the fore-feet; movements which had led Magendie, in similar experiments, to conclude that the sense of smell was not destroyed. Eschricht, in repeating this experiment, applied the ammonia to the anus. The animal then moved forward, contracted the sphincter repeatedly, and rubbed the anus with its feet ("prorsum animal procurrebat, celerrimus erat sphincteris motus et quomodo anterior pes antea nasum, ita posterior anum palpabat").[2] If the first experiment of Magendie showed that the sense of smell was retained, the experiment of Eschricht would equally show that the mucous membrane of the anus of the animal operated upon was endowed with olfactory sensibility.

Among the numerous experiments upon the higher orders of animals, in which the olfactory nerves have been divided, we may cite, as open to no objections, those of Vulpian and Philipaux, on dogs. It is well known that the sense of smell

[1] BERNARD, *Système nerveux*, Paris, 1858, tome ii., p. 229.

[2] ESCHRICHT, *De Functionibus primi et quinti Paris Nervorum in olfactoris Organo propriis.—Journal de physiologie*, Paris, 1826, tome vi., p. 350, note.

is usually very acute in these animals. Upon dividing or extirpating the olfactory bulbs, "after the animal had completely recovered, it was deprived of food for thirty-six or forty-eight hours; then, in its absence, a piece of cooked meat was concealed in a corner of the laboratory. Animals, successfully operated upon, then taken into the laboratory, never found the bait; and nevertheless, care had been taken to select hunting-dogs."[1] This experiment is absolutely conclusive; more so than those in which animals deprived of the olfactory bulbs were shown to eat fæces without disgust,[2] for this sometimes occurs in dogs that have not been mutilated.

Comparative anatomy shows that the olfactory bulbs are generally developed in proportion to the acuteness of the sense of smell. Pathological facts also show, in the human subject, that impairment or loss of the olfactory sense is coincident with injury or destruction of these ganglia. A large number of cases observed by Schneider, Rolfinck, Eschricht, Fahner, Valentin, Rosenmüller, Cerutti, and Pressat, between the years 1600 and 1837, are cited by Longet, in his elaborate treatise on the nervous system, in which the sense of smell was lost or impaired from injury to the olfactory nerves.[3] A case, reported by Hare, in 1821, showed total loss of smell from a disorder of the bones of the head. In this case, an examination was made after death and "the ethmoid (sieve-like) bone, which is naturally furnished with numerous minute openings for the transmission of branches of

[1] VULPIAN, *Leçons sur la physiologie générale et comparée du système nerveux*, Paris, 1866, p. 882, note.

[2] Schiff, in a very interesting series of observations on dogs, noted that these animals, deprived of the olfactory nerves, would drink their urine and eat food mixed with their fæces, while this was not observed in other animals, of the same litter, that had not been operated upon. The experiments were made with great care and upon young animals; and they show conclusively that the olfactory nerves preside over the sense of smell. (SCHIFF, *Der erste Hirnnerv ist der Geruchsnerv.—Untersuchungen zur Naturlehre, etc.*, Giessen, 1860, Bd. vi., S. 254, *et seq.*)

[3] LONGET, *Anatomie et physiologie du système nerveux*, Paris, 1842, tome ii., p. 88.

the olfactory nerves to the nose, was altogether condensed, and its openings obliterated; the two primordial trunks of the olfactory nerves, instead of exhibiting their usual ramifications, being suddenly blunted at their extensions from the substance of the brain; plainly showing, that all their branches essential to the sense of smell had been completely destroyed by the diseased bone."[1] This case is interesting as showing complete loss of smell after obliteration of the filaments passing through the cribriform plate of the ethmoid, to which, as we have stated, the term olfactory nerves properly belongs.

In addition to the instances just cited, a large number of cases of anosmia have been lately reported, which fully confirm the view that the olfactory nerves are the true and the only nerves of smell. Notta gives the histories, more or less complete, of twenty-four cases of this kind.[2] Dr. Ogle reports nine cases.[3] In nearly all of the cases on record, the general sensibility of the nostrils was not affected. In 1864, we had an opportunity of examining the following very remarkable case of gunshot-wound of the head, in which, among other injuries, the sense of smell was destroyed:

The patient was a soldier, twenty-three years of age, who was shot through the head with a rifle-ball, May 3, 1863. The ball entered on the left side, 1½ inch behind and ¾ of an inch below the outer canthus of the eye, emerging at nearly the corresponding point on the opposite side. Small pieces

[1] HARE, *A View of the Structure, Functions, and Disorders of the Stomach and Alimentary Organs*, London, 1821, p. 145.

[2] NOTTA, *Recherches sur la perte de l'odorat.—Archives générales de médecine*, Paris, Avril, 1870, p. 385.

[3] OGLE, *Anosmia; or Cases illustrating the Physiology and Pathology of the Sense of Smell.—Medico-Chirurgical Transactions*, London, 1870, Second Series, vol. xxxvii., p. 263. In his remarks upon the physiology of olfaction, Dr. Ogle advances the hypothesis that the sense of smell is acute in proportion to the development of pigment. He cites the remarks of Darwin on its absence or impairment in albino animals, the extraordinary development of the sense in certain of the dark-skinned races, etc.; but the facts adduced seem hardly sufficient to warrant the adoption of such a theory.

of bone were discharged from time to time for three months from openings in the posterior nares and the throat. He was examined May 10, 1864; when the wounds had healed, with falling in of the face over the left malar and nasal bones. He had then entirely lost the power of distinguishing odors. Upon applying acetic acid to the nostrils, he stated that he felt a prickling sensation, but no odor. Dilute ammonia produced a warm sensation. Chloroform gave no sensation. He had no sensation from the emanations of flowers. There was loss of general sensibility of the nasal mucous membrane on the left side, with diminished sensibility on the right side. He had a sensation, not very definite, when in water-closets, where (as he was told) the odor was very offensive, but experienced no sensation unless the emanations were very powerful. Before entering the army, he was a photographer by trade, and was familiar with the odors of acetic acid and ammonia. In this case, it is almost certain that the olfactory nerves had been divided, though other injuries undoubtedly existed.

Mechanism of Olfaction.

There can be no doubt at the present day with regard to the mechanism of the sense of smell. Substances endowed with odorous properties give off material emanations, which must come in contact with the olfactory membrane before their peculiar odor is appreciated. As we have seen, this membrane is situated high up in the nostrils, is peculiarly soft, is provided with numerous glands, by the secretions of which its surface is kept in proper condition, and possesses the peculiar nerve-terminations of the olfactory filaments.

In experimenting upon the sense of smell, it has been found quite difficult to draw the exact line of distinction between impressions of general sensibility and those which attack the special sense; or, in other words, between irritating and odorous emanations. Undoubtedly, the vapors of ammonia, acetic acid, nitric acid, etc., possess irritating prop-

erties which greatly overshadow their odorous qualities; and it was the neglect of this distinction that led to the errors of interpretation in the observations of Magendie. It is unnecessary, in this connection, to discuss the different varieties of odors recognized by some of the earlier writers, as the fragrant, aromatic, fetid, nauseous, etc., distinctions sufficiently evident from their mere enumeration; and it is plain enough that there are emanations, like those from delicately-scented flowers, which are easily recognizable by the sense of smell, while they make no impression upon the ordinary sensory nerves. The very marked individual differences in the delicacy of the olfactory organs in the human subject and in different animals is an evidence of this fact. Hunting-dogs recognize odors to which we are absolutely insensible; and certain races of men are said to possess a wonderful delicacy of the sense of smell. Like all of the other special senses, olfaction may be cultivated by attention and practice; as is exemplified in the delicate discrimination of wines, qualities of drugs, etc., by experts.

After what we have said concerning the situation of the true olfactory membrane in the upper part of the nasal fossæ and the necessity of particles impinging upon this membrane in order that their odorous properties may be appreciated, it is almost unnecessary to state that the passage of odorous emanations to this membrane by inspiring through the nostrils is essential to olfaction, so that animals or men, after division of the trachea, being unable to pass the air through the nostrils, are deprived of the sense of smell. The act of inhalation through the nose, when we wish to appreciate a particular odor, is an illustration of the mechanism by which the odorous particles may be brought at will in contact with the olfactory membrane. A very curious and interesting case illustrating the necessity of the free passage of air through the nostrils is detailed by Dr. Ogle. In this patient, there was adhesion of the posterior pillars of the fauces to the back of the pharynx, so that no air could pass through the nasal

fossæ. "While this is the case the man is completely unable to smell or to distinguish flavors, though he can still perfectly recognize true tastes, viz., sweet, salt, acid, bitter. This is his usual condition. But by an effort he is able momentarily to open the passage behind the velum, and when he does this he can for the time both smell and recognize flavors."[1]

It is a curious point to determine whether the sense of smell be affected by odors passing from within outward through the nasal fossæ. Persons who have offensive emanations from the respiratory organs usually are not aware, from their own sensations, of any disagreeable odor. This fact is explained by Longet on the supposition that the olfactory membrane becomes gradually accustomed to the odorous impression, and therefore it is not appreciated. This is an apparently satisfactory explanation, for we could hardly suppose that the direction of the emanations, provided they came in contact with the membrane, could modify their effects. He cites a case of cancer of the stomach, in which the vomited matters were exceedingly fetid. At first, the patient, when he expired the gases from the stomach through the nostrils, perceived a disagreeable odor at each expiration; but little by little this impression disappeared.[2]

Relations of Olfaction to the Sense of Taste.—The relations of the sense of smell to gustation are very intimate. In the appreciation of delicate shades of flavor, it is well known that the sense of olfaction plays so important a part, that it can hardly be separated from gustation. The common practice of holding the nose when disagreeable remedies are swallowed is another illustration of the connection between the two senses. In most of the cases of anosmia already referred to, reported by Notta and by Ogle, coincident with the loss of smell, there was inability to distinguish delicate flavors. The patients could only distinguish by the taste, sweet, saline,

[1] OGLE, *Anosmia.—Medico-Chirurgical Transactions*, London, 1870, p. 278.
[2] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 49.

acid, and bitter impressions. In four of the cases reported by Notta, there was complete loss of the sense of smell, the sense of taste remaining perfect.[1] In two of the cases reported by Ogle, the same fact was observed.[2] In three of the four cases, by Notta, the anosmia was due, in two, to polypus, and in one to coryza. In one case it was traumatic, and probably due to injury of the nerves. In one of the cases reported by Ogle, the anosmia was due to double facial paralysis, and in one, to coryza.

It is undoubtedly true that we lose the delicacy of the sense of taste when the sense of smell is abolished. The experiment of tasting wines blindfolded and with the nostrils plugged, and the partial loss of taste during a severe coryza, are sufficiently familiar illustrations of this fact. In the great majority of cases, when there is complete anosmia, the taste is sensibly impaired; and in the cases just referred to, in which this did not occur, it is probable that the savory emanations passed from the mouth to the posterior portion of the nasal fossæ, and that here the mucous membrane was not entirely insensible to special impressions. This explanation would certainly answer for the case in which the anosmia was due to facial palsy.

It is unnecessary, in this connection, to describe fully the reflex phenomena which follow impressions made upon the olfactory membrane. The odor of certain sapid substances, under favorable conditions, will produce an abundant secretion of saliva and even of gastric juice, as has been shown by experiments upon animals.[3] Other examples of the effects of odorous impressions of various kinds are sufficiently familiar.

[1] NOTTA, *Archives générales*, Paris, Avril, 1870.
[2] OGLE, *Medico-Chirurgical Transactions*, London, 1870.
[3] See vol. ii., Digestion, p. 228.

CHAPTER III.

OPTIC NERVES—ANATOMY OF THE EYE.

General considerations—Physiological anatomy of the optic nerves—General properties of the optic nerves—Physiological anatomy of the eyeball—Diameters of the eyeball—Sclerotic coat—Cornea—Membrane of Descemet, or of Demours—Ligamentum iridis pectinatum—Choroid coat—Uvea—Ciliary processes—Ciliary muscle—Iris—Canal of Schlemm, or circular venous sinus—Pupillary membrane—Retina—Jacob's membrane—Crystalline lens—Suspensory ligament of the lens—Zone of Zinn—Aqueous humor—Chambers of the eye—Vitreous humor—Summary of the anatomy of the globe.

VISION, one of the most important and delicate of the special senses, involves, not only the impressions conveyed by the optic nerves to the brain, but the action of accessory parts, the structure of which is exceedingly complex. The integrity of these parts is absolutely essential to perfect vision; and they are liable to be injured by disease or otherwise in a great variety of ways. At the present day, the treatment of diseases of the eye is, to a great extent, confined to those who have made its physiology and pathology a special study; and, thanks to the labors of Helmholtz, Donders, Von Graefe, and a host of other writers, ophthalmology ranks among the most advanced of the subdivisions of medical science, with a literature exceedingly full and exact.

Probably there is no department of medicine, in which the principle, that the true basis of pathology is a thorough knowledge of anatomy and physiology, is more completely carried out than in ophthalmology. In many of the elaborate works on diseases of the eye, the anatomy of the parts and the physiology of vision are treated of very minutely. To

such works, those specially devoted to the subject will refer; particularly as, in such treatises, the bearings of physiology upon pathology and treatment are fully considered. Our section on the subject of vision is not intended to meet the wants of the ophthalmologist, nor does it seem desirable that it should. Our aim is to treat of the anatomy and physiology of the organs of vision so as to make the subject clear, merely as far as its physiology is concerned. In doing this, we shall omit certain anatomical details, as well as most of the elaborate mathematical formulæ of modern physicists, and all researches of a purely historical interest, which, if fully dwelt upon, would swell the chapters on vision to the dimensions of a large volume.

The chief important points to be considered in the physiology of vision are the following:

1. The physiological anatomy and the general properties of the optic nerves.
2. The physiological anatomy of the parts essential to correct vision.
3. The laws of refraction, diffusion, etc., bearing upon the physiology of vision.
4. The action of the different parts of the eye in the production and appreciation of correct images.
5. Binocular vision.
6. The physiological anatomy and the functions of accessory parts, as the muscles which move the eyeball.
7. The physiological anatomy and the functions of the parts which protect the eye, as the lachrymal glands, eyelids, etc.

Physiological Anatomy of the Optic Nerves.—The optic nerves, or tracts, take their origin, each by two principal roots of white matter and a few filaments from what is described as the gray root, chiefly from the tubercula quadrigemina, but in part from those portions of the encephalon over which the nerves pass to go to the eyes. The internal white root arises

from the posterior, and the external white root, which is the larger, from the anterior tuberculum. The gray root is situated in front of and above the optic commissure, and is a dependence of the gray matter which covers the internal surface of the optic thalamus. It arises from the gray matter constituting the anterior floor of the third ventricle, in the form of delicate filaments which join the optic nerves at this point.[1]

The apparent origin of these nerves is from the tubercula quadrigemina, receiving filaments from the corpora geniculata, the optic thalami, the peduncles of the cerebrum, the anterior substantia perforata, the tuber cinereum, and the lamina terminalis. It has thus far been found impossible to trace all these roots to their true origin in the cerebral substance; but experiments upon the lower animals, in which it has been shown that the sense of sight is completely abolished by destruction of the tubercula quadrigemina (bigemina, in birds), show that the origin of the filaments that preside over vision is, in all probability, from these bodies.

The two principal roots unite above the external corpus geniculatum, forming a flattened band, which takes an oblique course around the under surface of the crus cerebri to the optic commissure. This is usually called the optic tract, in contradistinction to the optic nerve, which is described as arising from the optic commissure.

The optic commissure, or chiasm, is situated just in front of the corpus cinereum, resting on the olivary process of the sphenoid bone. As its name implies, this is the point of union between the nerves of the two sides. At the commissure, the fibres from the optic tracts take three directions; and, in addition, the commissure contains filaments passing from one eye to the other, which have no connection with the optic tracts. The four sets of fibres in the optic commissure are as follows:

1. Decussating fibres, passing from the optic tract upon

[1] SAPPEY, *Traité d'anatomie*, Paris, 1871, tome iii., p. 251.

either side to the eye of the opposite side. The greatest part of the fibres take this direction. Their relative situation is internal.

2. External fibres, much less numerous than the preceding, which pass from the optic tract to the eye upon the same side.

3. Fibres, situated on the posterior boundary of the commissure, which pass from one optic tract to the other and do not go to the eyes. These fibres are scanty, and, according to Sappey, are sometimes wanting.[1]

4. Fibres, situated on the anterior border of the commissure, more numerous than the preceding, which pass from one eye to the other, and which have no connection with the optic tracts.[2]

It is probable, reasoning chiefly from cases of cerebral injury or disease, that the filaments from the optic tracts upon the two sides are connected with distinct portions of

[1] SAPPEY, *Traité d'anatomie*, Paris, 1871, tome iii., p. 254.

[2] Within the last few years, the old idea that the optic nerves make a complete decussation at the commissure has been revived. In two very elaborate articles on this subject, which have just appeared (1873) in Graefe's Archiv, by Mandelstamm and by Michel, the authors, after referring to the anatomical researches of Biesiadecki, in 1861, and of Pawlowsky, in 1869, assume to have confirmed their observations, and to have demonstrated that the nerves decussate completely at the commissure and are each distributed exclusively to the eye of the opposite side. Purely anatomical researches upon such a delicate point as this are uncertain; and it is with the aid of pathological observations, that positive conclusions have been reached. With the views advanced by Mandelstamm and by Michel, it is perhaps possible to explain cases of hemiopsia due to tumors situated at some parts of the chiasm, but not hemiopsia following deep-seated injury or disease of the brain near the origin of one of the optic tracts. Two such cases we shall quote from Drs. Keen and Thomson (see page 41), and these are sufficient to lead us to doubt the accuracy of the view of complete decussation, at least until it shall have received full confirmation. The new view, however, is fully discussed in the following articles, to which the reader is referred:

MANDELSTAMM, *Ueber Sehnervenkreuzung und Hemiopie.—Archiv für Ophthalmologie*, Berlin, 1873, Bd. xix., S. 39, *et seq.*

MICHEL, *Ueber den Bau des Chiasma nervorum opticorum.*—Ibid., S. 59, *et seq.*

the retina; and two pathological cases have lately been reported by Drs. Keen and Thomson, of Philadelphia, which go to show that this is the fact, and which illustrate certain interesting points in connection with the decussation of the nerves. One was a case of gunshot-wound of the head with severe injury of the brain-substance. This case presented, immediately after the injury, unconsciousness and partial paralysis of the right arm and right leg, which lasted two or three months. About a year after, the paralysis had almost entirely disappeared, but the memory was somewhat impaired. Upon careful examination of the eyes, it was ascertained that the field of vision was divided in each eye by a vertical line passing through its centre. In the right eye, the inner half of the retina, beginning at the inner border of the macula lutea, was entirely insensible to light. In the left eye, the outer half of the retina, beyond the macula, was insensible to light. No pathological appearances were observed on examining the retinæ with the ophthalmoscope. The second case, reported by Dr. W. Thomson, presented the same condition following partial hemiplegia, the result of sunstroke. The peculiar affection of vision in these cases, called hemiopsia, especially as illustrated in the first case, reported by Dr. Keen, can be explained by assuming the following as the course of the decussating fibres of the optic tracts: From the left side of the encephalon, visual fibres pass to the right eye, supplying the inner mathematical half of the retina, from a vertical line passing through the macula lutea. Visual fibres also pass to the left eye, supplying the outer half of the retina, beginning at the macula lutea. The macula lutea, then, and not the point of entrance of the optic nerve, is in the line of division of the visual field. The outer half of the left and the inner half of the right retina are supplied by fibres from the left side; and the outer half of the right and the inner half of the left retina are supplied from the right side. Though this anatomical arrangement has not been actually demonstrated, it is rendered ex-

ceedingly probable by pathological cases like those just cited.[1] In the case reported by Dr. Keen, the left side of the brain was injured, as the paralysis occurred in the right leg and arm.

With the exception of the few filaments derived from what have been described as the gray roots, the fibres of the optic tracts and the optic nerves are of the medullated variety, and present no differences in structure from the ordinary cerebro-spinal nerves.

The optic commissure is covered with a fibrous membrane, and is consequently more resisting than the optic tracts. From its anterior and outer border, arise the optic nerves, which take a curved direction to the eyes. The nerves are rounded, and are enclosed in a double fibrous sheath derived from the dura mater and the arachnoid. They pass into the orbit upon the two sides by the optic foramina, and penetrate the sclerotic at the posterior, inferior, and internal portion of the globe. As the nerves enter the globe, they lose their coverings from the dura mater and arachnoid. The sheath derived from the dura mater is adherent to the periosteum of the orbit at the foramen opticum, and when it reaches the globe it fuses with the sclerotic coat. Just before the nerves penetrate the globe, they each present a well-marked constriction. At the point of penetration, there is a thin but strong membrane, presenting numerous perforations for the passage of the nervous filaments. This membrane, the lamina cribrosa, is in part derived from the sclerotic, and in part, from the coverings of the individual nerve-fibres, which lose their investing membranes at this point. In the interior of each eye, there is a little, mammillated eminence, formed by the united fibres of the nerve. The retina, with which the optic nerve is connected, will be described as one of the coats of the eye.

[1] KEEN AND THOMSON, *Gunshot-Wound of the Brain, followed by Fungus Cerebri, and Recovery with Hemiopsia*, Extracted from the *Photographic Review of Medicine and Surgery*, February, 1871.

In the centre of the optic nerve, is a minute canal, lined by fibrous tissue, in which is lodged the central artery of the retina and its corresponding vein, with a delicate, nervous filament from the ophthalmic ganglion. The vessels penetrate the optic nerve a little (from $\frac{1}{8}$ to $\frac{3}{4}$ of an inch) behind the globe. The central canal does not exist behind these vessels.

General Properties of the Optic Nerves.—There is very little to be said regarding the general properties of the optic nerves, except that they are undoubtedly the only nerves capable of conveying to the cerebrum the special impressions of sight, and that they are not endowed with general sensibility.

That the optic nerves are the only nerves of sight, there can be no doubt. Their division or injury always involves loss or impairment of vision, directly corresponding with the lesion.[1] It is interesting, however, to note that they are absolutely insensible to ordinary impressions. "We can, in a living animal, pinch, cauterize, cut, destroy in any way the optic nerve without giving rise to the slightest painful sensation; whether it be taken before or after its decussation, it seems completely insensible in its entire length."[2]

Not only are the optic nerve and retina insensible to pain, but any irritation produces the impression of light. This was stated in the remarkable paper, *Idea of a New Anatomy of the Brain*, printed by Charles Bell, in 1811.[3] A few years later, Magendie, in operating for cataract, passed the

[1] In 1828, Magendie, influenced probably by his favorite theory that the fifth pair of nerves was necessary to the perfect operation of all the special senses, reported two cases of atrophy of the optic nerves, without complete loss of sight, and assumed, as a possibility, that sight might be retained to a limited degree, when the optic nerves had been gradually destroyed. This view does not merit discussion, and is simply one of the curiosities of physiological literature. (MAGENDIE, *La vue peut-elle être conservée malgré de destruction des nerfs optiques?—Journal de physiologie*, Paris, 1828, tome viii., p. 27.)

[2] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 479.

[3] BELL, *Idea of a New Anatomy of the Brain*, London, 1811.—*Documents and Dates of Modern Discoveries in the Nervous System*, London, 1839, p. 43.

needle to the bottom of the eye and irritated the retina, in two persons. The patients experienced no pain, but the impression of flashes of light.[1] The insensibility of the optic nerves has also been repeatedly noted in surgical operations in which the nerves have been exposed.[2] If a current of galvanism be passed through the optic nerves, a sensation of light is experienced.[3] The same phenomenon is observed when the eyeball is pressed upon or contused, a fact which is sufficiently familiar.

Physiological Anatomy of the Eyeball.

The eyeball is a spheroidal body, partially embedded in a cushion of fat in the orbit, protected by the surrounding bony structure and the eyelids, its surface bathed by the secretion of the lachrymal gland, and movable in various directions by the action of certain muscles. When the axis of the eye is directed forward, the globe has the form of a sphere in its posterior five-sixths, with the segment of a smaller sphere occupying its anterior sixth. The segment of the smaller sphere, bounded externally by the cornea, is more prominent than the rest of the surface.

The eyeball is made up of several coats enclosing certain refracting media. The external coat is the sclerotic, covering the posterior five-sixths, which is continuous with the cornea, covering the anterior sixth. This is a dense, opaque, fibrous membrane, for the protection of the inner coats and contents. The cornea is dense, resisting, and perfectly transparent. The muscles that move the globe of the eye are attached to the sclerotic.

Were it not for the prominence of the cornea, the eyeball would present very nearly the form of a perfect sphere, as

[1] MAGENDIE, *Sur l'insensibilité de la rétine de l'homme.—Journal de physiologie*, Paris, 1825, tome v., p. 37, *et seq.*

[2] LONGET, *Physiologie*, Paris, 1869, tome iii., p. 479.

[3] MEYER, *Electricity in its Relations to Practical Medicine*, New York, 1869, p. 69.

will be seen by the following measurements of its various diameters; but the prominence of its anterior sixth gives the greatest diameter in the antero-posterior direction.

The form and dimensions of the globe are subject to considerable variations after death, by evaporation of the humors, emptying of vessels, etc., and there is no way in which the normal conditions can be restored.[1] The most exact measurements are those made by Sappey. As an illustration of the post-mortem changes in the eye, Sappey mentions comparative measurements made three hours and twenty-four hours after death, the results of which presented very considerable differences.

In measurements made by Sappey, apparently with great care and accuracy, from one to four hours after death, of the eyes of twelve adult females and fourteen adult males of different ages, the following mean results were obtained:[2]

	Diameters—Inch.			
	Ant.-post.	Transverse.	Vertical.	Oblique.
Mean of 12 females, from 18 to 81 years of age..	0·941	0·911	0·905	0·937
Mean of 14 males, from 20 to 79 years of age.....	0·968	0·941	0·925	0·949

From these results, it is seen that the diameters are all less in the female than in the male. The antero-posterior diameter is the greatest of all, and the vertical diameter is the least. The measurements at different ages, not cited in the table just given, show that the excess of the antero-posterior diameter over the others is diminished by age.

Sclerotic Coat.—The sclerotic is the dense, opaque, fibrous covering of the posterior five-sixths of the eyeball. Its thickness is different in different portions. At the point of pene-

[1] It is for the above reason that we reject the measurements made by Krause, which are so often cited in works on the anatomy and physiology of the eye.

[2] SAPPEY, *Traité d'anatomie*, Paris, 1871, tome iii., p. 708.

tration of the optic nerve, it measures $\frac{1}{25}$ of an inch. It is thinnest at the middle portion of the eye, measuring about $\frac{1}{60}$ of an inch, and is a little thicker again near the cornea. This membrane is composed chiefly of bundles of ordinary connective tissue. The fibres are slightly wavy, and arranged in flattened bands, which are alternately longitudinal and transverse, giving the membrane a lamellated appearance, though it cannot be separated into distinct layers. Mixed with these bands of connective-tissue fibres, are numerous small fibres of elastic tissue. The vessels of the sclerotic are scanty. They are derived from the ciliary vessels and those of the muscles of the eyeball. The tissue of the sclerotic yields gelatine on boiling.

Cornea.—The cornea is the transparent membrane which covers about the anterior sixth of the globe of the eye. As before remarked, this is the most prominent portion of the eyeball, and is in the form of a segment of a sphere attached by its borders to the segment of the larger sphere formed by the sclerotic. The thickness of the cornea is about $\frac{1}{30}$ of an inch in its central portion, and about $\frac{1}{25}$ of an inch near its periphery. Its substance is composed of transparent fibres, arranged in incomplete layers, something like the layers of the sclerotic. It yields chondrine, instead of gelatine, on boiling.

Upon the external, or convex surface of the cornea, are several layers of delicate, transparent, nucleated epithelium. The most superficial cells are flattened; the middle cells are rounded; and the deepest cells are elongated and arranged perpendicularly. These cells become slightly opaque and whitish after death. Just beneath the epithelial covering of the cornea, is a very thin, transparent membrane, described by Bowman under the name of the "anterior elastic lamella."[1] This membrane, with its cells, is a continuation of the conjunctiva.

[1] TODD AND BOWMAN, *The Physiological Anatomy and Physiology of Man*, Philadelphia, 1857, p. 404.

The proper corneal membrane is composed of excessively pale, flattened bundles of fibres, interlacing each other in every direction. Their arrangement is lamellated, though they cannot be separated into complete and distinct layers. Between the bundles of fibres, lie a great number of stellate, anastomosing, connective-tissue corpuscles. In these cells and in the intervals between the fibres, there is a considerable quantity of transparent liquid. The fibres constituting the substance of the cornea are continuous with the fibrous structure of the sclerotic, from which they cannot be separated by maceration. At the margin of the cornea, the opaque fibres of the sclerotic became abruptly transparent. The corneal substance is very tough, and will resist a pressure sufficient to rupture the sclerotic.

Upon the posterior, or concave surface of the cornea, is the membrane of Descemet, or of Demours, elastic, transparent, structureless, rather loosely attached, and covered with a single layer of regularly-polygonal, nucleated epithelium. At the circumference of the cornea, a portion of this membrane passes to the anterior surface of the iris, in the form of numerous processes which constitute the ligamentum iridis pectinatum; a portion passes into the substance of the ciliary muscle, and a portion is continuous with the fibrous structure of the sclerotic.

In the adult, the cornea is almost without blood-vessels, but in fœtal life it presents a rich plexus extending nearly to the centre. These disappear, however, before birth, leaving a very few delicate, looped vessels at the extreme edge.

A great deal of anatomical interest has lately been attached to the cornea, from researches showing the termination of the fine nerve-fibres in the nuclei of the posterior layer of the epithelium of its convex surface,[1] and the investigation of the "lymph-spaces," by the use of certain reagents, the demonstration of the so-called "wandering cells,"

[1] See vol. iv., Nervous System, p. 45.

etc., points that we do not propose to consider. It is well known that the surface of the cornea is exquisitely sensitive.

Choroid Coat.—Calling the sclerotic and the cornea the first coat of the eyeball, the second is the choroid, with the ciliary processes, the ciliary muscle, and the iris. This was called by the older anatomists the uvea, a name which was later applied, sometimes to the entire iris, and sometimes to its posterior, or pigmentary layer. We shall describe, however, the choroid and ciliary processes together as the second coat, and then take up the ciliary muscle and the iris.

The choroid is distinguished from the other coats of the eye by its dark color and its great vascularity. It occupies that portion of the eyeball corresponding to the sclerotic. It is perforated posteriorly by the optic nerve, and is connected in front with the iris. It is very delicate in its structure, and is composed of two or three distinct layers. Its thickness is from $\frac{1}{160}$ to $\frac{1}{96}$ of an inch. Its thinnest portion is at about the middle of the eye. Posteriorly, it is a little thicker. Its thickest portion is at its anterior border.

The external surface of the choroid is connected with the sclerotic by vessels, nerves (the long ciliary arteries and the ciliary nerves), and very loose connective tissue. This is sometimes called the membrana fusca, though it can hardly be called a distinct layer. It contains, in addition to the vessels, nerves, and fibrous tissue, a few irregularly-shaped pigment-cells.

The rest of the choroid is composed of two distinct layers; an external, vascular, and an internal, pigmentary layer. The vascular layer consists of numerous arteries, veins, and capillaries, arranged in a peculiar manner. The layer of capillary vessels, which is internal, is sometimes called the middle layer of the choroid, or the tunica Ruyschiana. The arteries, which are derived from the posterior short ciliary arteries and are connected with the capillary plexus, lie just beneath the pigmentary layer. The plexus of capillaries is closest at the

posterior portion of the membrane. The veins are external to the other vessels. They are very numerous and are disposed in curves converging to four trunks. This arrangement gives the veins a very peculiar appearance, and they have been called the vasa vorticosa.

The pigmentary portion is composed, over the greatest part of the choroid, of a single layer of regularly-polygonal cells, somewhat flattened, measuring from $\frac{1}{2000}$ to $\frac{1}{1500}$ of an inch in diameter. These cells are filled with pigmentary granulations of uniform size, and give to the membrane its characteristic dark-brown or chocolate color. The pigmentary granules in the cells are less numerous near their centre, where a clear nucleus can readily be observed. In the anterior portion of the membrane, in front of the anterior limit of the retina, the cells are smaller, more rounded, more completely filled with pigment, and present several layers. Beneath the layer of hexagonal pigment-cells, the intervascular spaces of the choroid are occupied by stellate pigment-cells.

Ciliary Processes.—The anterior portion of the choroid is arranged in the form of folds, or plaits projecting internally, called the ciliary processes. The largest of these folds are about $\frac{1}{10}$ of an inch in length. They are from sixty to eighty in number. The larger folds are of nearly uniform size, and are regularly arranged around the margin of the crystalline lens. Between these folds, which constitute about two-thirds of the entire number, are smaller folds, lying, without any regular alternation, between the larger. Within the folds, are received corresponding folds of the thick membrane, continuous anteriorly with the hyaloid membrane of the vitreous humor, called the zone of Zinn.

The ciliary processes present blood-vessels, which are somewhat larger than those of the rest of the choroid. The pigmentary cells are smaller and are arranged in several layers. The anterior border of the processes is free, and contains little or no pigment.

Ciliary Muscle.—This muscle, formerly known as the ciliary ligament, and now sometimes called the tensor of the choroid, is almost universally recognized by physiologists as the agent for the accommodation of the eye to vision at different distances. Under this view, the ciliary muscle is an organ of great importance, and it is essential, in the study of accommodation, to have an exact idea of its relations to the coats of the eye and to the crystalline lens. For this reason, we shall describe its arrangement as exactly as possible.

The form and situation of the ciliary muscle are as follows: It surrounds the anterior margin of the choroid, in the form of a ring about $\frac{1}{8}$ of an inch wide and $\frac{1}{50}$ of an inch in thickness at its thickest portion, which is its anterior border. It becomes thinner from before backward, until its posterior border apparently fuses with the fibrous structure of the choroid. It is semitransparent and of a grayish color. Its situation is just outside of the ciliary processes, these processes projecting in front of its anterior border about $\frac{1}{25}$ of an inch.

Regarding the anterior border of this muscle as its origin and the posterior border as its insertion, it arises in front from the circular line of junction of the cornea and sclerotic, from the border of the membrane of Descemet and the ligamentum iridis pectinatum. Its fibres, which are chiefly longitudinal, pass backward and are lost in the choroid, extending somewhat farther back than the anterior limit of the retina. In addition, a net-work of circular muscular fibres has been described lying over the anterior portion of the ciliary body, at the periphery of the iris, beneath the longitudinal fibres; but these are regarded by Donders as simple continuations of the innermost layers of the longitudinal fibres, which gradually assume a circular direction, not meriting description as a separate muscle.[1] Some of these fibres have an oblique direction.

[1] DONDERS, *On the Anomalies of Accommodation and Refraction of the Eye*, The New Sydenham Society, London, 1864, p. 25.

Although there was formerly considerable discussion with regard to the structure of the ciliary ligament, or muscle, there can now be scarcely any doubt of the fact that it is composed mainly of muscular fibres. These fibres, anatomically considered, belong to the non-striated, or involuntary variety. They are pale, present numerous oval, longitudinal nuclei, and have no striæ.

It is evident, from the arrangement of the fibres of the ciliary muscle, that its action must be to approximate the border of connection of the sclerotic and cornea and the circumference of the choroid, compressing the vitreous humor and relaxing the suspensory ligament of the crystalline lens. We shall see farther on that this action enables the lens to change its form, and probably adapts its curvature to vision at different distances. The nerves of the ciliary muscle are derived from the long and the short ciliary.

Iris.—The iris corresponds to the diaphragm of optical instruments, except that its orifice is capable of dilatation and contraction. It is a circular membrane, situated just in front of the crystalline lens, with a round perforation, the pupil, near its centre. It is called the uvea by some anatomists, a name that was formerly applied to the iris and choroid together.

The attachment of the greater circumference of the iris is to the line of junction of the cornea and sclerotic, near the origin of the ciliary muscle, the latter passing backward to be inserted into the choroid, and the former passing directly over the crystalline lens. The diameter of the iris is about half an inch. The pupil is subject to considerable variations in size. When at its medium of dilatation, its diameter is from $\frac{1}{8}$ to $\frac{1}{4}$ of an inch. The pupillary orifice is not in the mathematical centre of the iris, but is situated a little to the nasal side. The thickness of the iris is a little greater than that of the choroid, but is unequal in different parts, the membrane being thinnest at its great circumference and its pupillary

border, and thickest at about the junction of its inner third with the outer two-thirds. It slightly projects anteriorly and divides the space between the lens and the cornea into two chambers, anterior and posterior, the anterior chamber being much the larger. Taking advantage of a property of the crystalline lens, called fluorescence, which enables us, by concentrating upon it a blue light, to see the boundaries in the living eye, Helmholtz has demonstrated that the posterior surface of the iris and the anterior surface of the lens are actually in contact,[1] except, perhaps, for a certain distance near the periphery of the iris. This being the case, the posterior chamber is very small, and only exists near the margins of the lens and the iris.

The color of the iris is very different in different individuals. Its anterior surface is generally very dark near the pupil, and presents colored radiations toward its periphery. Its posterior surface is of a dark-purple color, and is covered with pigmentary cells.

The entire iris presents three layers. The anterior layer is continuous with the membrane of the aqueous humor. At the great circumference, it presents little fibrous prolongations, forming a delicate dentated membrane, called the ligamentum iridis pectinatum. The membrane covering the general anterior surface of the iris is extremely thin, and is covered by cells of tessellated epithelium. Just beneath this membrane, are a number of irregularly-shaped pigmentary cells.

The posterior layer of the iris is very thin, easily detached from the middle layer, and contains numerous small cells exceeding rich in pigmentary granules. Some anatomists recognize this membrane only as the uvea.[2]

The middle layer constitutes by far the greatest part of

[1] HELMHOLTZ, *Des progrès récents dans la théorie de la vision.—Revue des cours scientifiques*, Paris, 1868–1869, tome vi., p. 217.

[2] The name uvea was applied, at one time, to the choroid with the iris, again to the iris alone, and again to the posterior, or pigmentary layer of the iris. To avoid confusion, this term will not be again used.

the substance of the iris. It is composed of connective tissue, muscular fibres of the non-striated variety, numerous blood-vessels, and, probably, nerve-terminations. From a physiological point of view, the arrangement of the muscular fibres is the most interesting. Directly surrounding the pupil, forming a band about $\frac{1}{48}$ of an inch in width, is a layer of non-striated muscular fibres, called the sphincter of the iris. The existence of these fibres is admitted by all anatomists. It is different, however, for the radiating muscular fibres. Most anatomists describe, in addition to the sphincter, fibres of the same variety, which can be traced from near the great circumference of the iris almost to its pupillary border, lying both in front of and behind the circular fibres, which are, as it were, enclosed between them. A few observers deny that these fibres are muscular; but they recognize a thick muscular layer surrounding the arteries of the iris. This is merely a question of observation; but the weight of anatomical authority is greatly in favor of the existence of the radiating fibres; and their presence explains certain of the phenomena of dilatation of the iris which would otherwise be difficult to understand.

The blood-vessels of the iris are derived from the arteries of the choroid, the long posterior ciliary, and the anterior ciliary arteries. The long ciliary arteries are two branches, running along the sides of the eyeball between the sclerotic and choroid, to form, finally, a circle surrounding the iris. The anterior ciliary arteries are derived from the muscular branches of the ophthalmic. They penetrate the sclerotic a little behind the iris, and join the long ciliary arteries in the vascular circle. From this circle, the vessels branch and pass into the iris, to form a smaller arterial circle around the pupil. The veins from the iris empty into a circular sinus situated at the junction of the cornea with the sclerotic. This is sometimes spoken of as the circular venous sinus, or the canal of Schlemm.

The nerves of the iris are the long ciliary, from the fifth cranial, and the short ciliary, from the ophthalmic ganglion.

Pupillary Membrane.—At a certain period of fœtal life, the pupil is closed by a membrane connected with the lesser circumference of the iris, called the pupillary membrane. This is not distinct during the first months; but, between the third and the fourth months, it is readily seen, and is most apparent at the sixth month. The membrane is thin, transparent, and completely separates the anterior from the posterior chamber of the eye. It is provided with vessels derived from the arteries of the iris, anastomosing with each other and turning back in the form of loops near the centre. At about the seventh month, it begins to give way at the centre, gradually atrophies, and generally scarcely a trace of it can be seen at birth.

Retina.—The retina is described by anatomists as the third tunic of the eye. It is closely connected with the optic nerve, and the most important structures entering into its composition are probably continuous with prolongations from the nerve-cells. This is the membrane endowed with the special sense of sight, the other structures in the eye being accessory.

There is probably no special tissue in the organism that has been the subject of anatomical investigations so minute and elaborate as those made of late years upon the retina. This membrane is divided by some observers into no less than eight distinct layers, each of which may be found described in special treatises, with the greatest minuteness of detail. It is true that a knowledge of the physiological anatomy of the retina is indispensable, in the study of vision; but, in the complex structure of this membrane, there are parts that seem to be the actual recipients of visual impressions, while others are more or less accessory. In our anatomical descriptions, we shall endeavor to avoid the tediousness of unnecessary detail, and shall treat elaborately of those anatomical elements only that are directly concerned in the sense of sight.

If the sclerotic and choroid be removed from the eye un-

der water, the retina is seen, in perfectly fresh specimens, in the form of an exceedingly delicate and transparent membrane covering the posterior portion of the vitreous humor. A short time after death, it becomes slightly opaline. It extends over the posterior portion of the eyeball to a distance of about $\frac{1}{15}$ of an inch behind the ciliary processes. When torn from its anterior attachment, it presents a finely-serrated edge, called the ora serrata. This edge adhères very closely, by mutual interlacement of fibres, to the zone of Zinn. In the middle of the membrane, its thickness is about $\frac{1}{120}$ of an inch. It becomes thinner near the anterior margin, where it measures only about $\frac{1}{300}$ of an inch. Its external surface is in contact with the choroid, and its internal, with the hyaloid membrane of the vitreous humor.

The optic nerve penetrates the retina about $\frac{1}{8}$ of an inch within and $\frac{1}{25}$ of an inch below the antero-posterior axis of the globe, presenting, at this point, a small, rounded elevation upon the internal surface of the membrane, perforated in its centre for the passage of the central artery of the retina. At from $\frac{1}{12}$ to $\frac{1}{8}$ of an inch external to the point of penetration of the nerve, is an elliptic spot, its long diameter being horizontal, about $\frac{1}{8}$ of an inch long and $\frac{1}{36}$ of an inch broad, called the yellow spot of Sömmerring, or the macula lutea. In the centre of this spot, is a depression, called the fovea centralis. This depression is exactly in the axis of vision. The yellow spot exists only in man and the quadrumana.

The layers of the retina which present the greatest physiological interest are the external layer, formed of rods and cones, the layer of nerve-cells, and the filaments which connect the rods and cones with the cells. These are the only anatomical elements of the retina, as far as we know, that are directly concerned in the reception of optical impressions, and they will be described rather minutely, while the intermediate layers will be considered more briefly.

Most modern anatomists recognize eight distinct layers in the retina, as follows:

1. An external layer, situated next the choroid, called Jacob's membrane, the bacillar membrane, or the layer of rods and cones.
2. The external granule-layer.
3. The inter-granule layer (cone-fibre plexus, of Hulke).
4. The internal granule-layer.
5. The granular layer.
6. The layer of nerve-cells (ganglion-layer).
7. The expansion of the fibres of the optic nerve.
8. The limitary membrane.

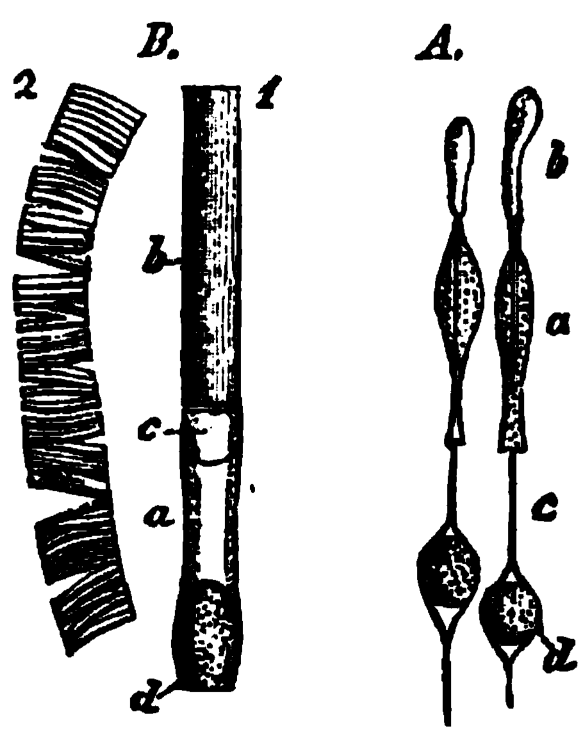
The layer of rods and cones is composed of rods, or cylinders, extending through its entire thickness, closely packed, and giving to the external surface a regular, mosaic appearance; and, between these, are a greater or less number of flask-shaped bodies, the cones. This layer is about $\frac{1}{350}$ of an inch in thickness at the middle of the retina; $\frac{1}{400}$ of an inch, about midway between the centre and the periphery; and, near the periphery, about $\frac{1}{450}$ of an inch. At the macula lutea, the rods are wanting, and the layer is composed entirely of cones, which are here very much elongated. Over the rest of the membrane, the rods predominate, and the cones become less and less numerous toward the periphery.

The rods are regular cylinders, their length corresponding to the thickness of the layer, terminating above in truncated extremities, and below in points, which are probably continuous with the filaments of connection with the nerve-cells, though they have been actually traced only into the external granule-layer. Their diameter is about $\frac{1}{13000}$ of an inch. They are clear, of rather a fatty lustre, soft and pliable, but somewhat brittle, and so alterable that they are with difficulty seen in a natural state. They should be examined in perfectly fresh preparations, moistened with liquid from the vitreous humor or with serum. Their intimate structure, as well as that of the cones, has recently been very closely studied, especially by German anatomists.[1] When perfectly fresh, it

[1] An excellent review of the recent investigations into the anatomy of the

is difficult to make out any thing but an entirely homogeneous structure; but shortly after death each rod seems to be divided by a delicate line into an outer and an inner segment, the outer being a little the longer. At the upper extremity of the inner segment, is a hemispherical body, with its convexity presenting inward, called the lentiform body (*linsenförmiger Körper*). The entire inner segment is somewhat granular, and often presents a granular nucleus at its inner extremity. The outer segment apparently differs in its constitution from the inner segment, and is not similarly affected by reagents. Treated with dilute acetic acid, the outer segment becomes broken up transversely into thin disks. These points in the anatomy of the rods are referred to particularly, for the reason that they have lately been used as an anatomical basis for a theory of the perception of colors.[1] They can be readily understood by reference to Fig. 2.

FIG. 2.



From the monkey.—*A*. Rods, after maceration in iodized serum, the outer segment (*b*) truncated, the inner segment (*a*) coagulated, granular, and somewhat swollen; *c*, filament of the rods; *d*, nucleus. *B*. Rods from the frog. 1. Fresh, magnified 500 diameters. *a*, inner segment; *b*, outer segment; *c*, lentiform body; *d*, nucleus. 2. Treated with dilute acetic acid and broken up into plates, magnified 1,000 diameters. Taken from Schultze's figures. (KÖLLIKER, *Handbuch der Gewebelehre*, Leipzig, 1867, S. 670.)

The cones are probably of the same constitution as the rods, but that portion called the inner segment is pyriform. The straight portion above (the outer segment) is sometimes called the cone-rod. The entire cones are about half the

retina is to be found in the *Journal de l'anatomie*, Paris, 1869, tome vi., pp. 488, 543, 648. As regards the structure of the rods and cones, the views of Schultze are now pretty generally accepted by anatomists. (SCHULTZE, *Ueber Stäbchen und Zapfen der Retina.—Archiv für mikroskopische Anatomie*, Bonn, 1867, Bd. iii., S. 215, *et seq.*)

[1] ZENKER, *Versuch einer Theorie der Farben-Perception.—Archiv für mikroscopische Anatomie*, Bonn, 1867, Bd. iii., S. 248, *et seq.*

length of the rods, and occupy the inner portion of the layer. The outer segment is, in its constitution, precisely like the outer segment of the rods. The inner segment is slightly granular and contains a nucleus. The cones are connected below with filaments passing into the deeper layers of the retina. The arrangement of the rods and cones is seen in Fig. 3, which shows the different layers of the retina.

At the fovea centralis, the external layer is composed entirely of immensely elongated cones, with no rods. These are slightly increased in thickness at the macula lutea, but are diminished again in thickness, by about one-half, at the fovea centralis.[1] At the fovea, the optic nerve-fibres are wanting; the ganglion-cells, which are elsewhere over the retina in a single layer, here present from six to eight layers, except at the very centre, where there are but three layers. Of the layers between the cones and the ganglion-cells, the external granule-layer and the inter-granule layer (cone-fibre plexus) remain, in the fovea, while the internal granule-layer and the granular (molecular) layer are wanting. At the fovea, indeed, those elements of the retina which may be regarded as purely accessory seem to disappear, leaving only the structures that are concerned directly in the reception of visual impressions.

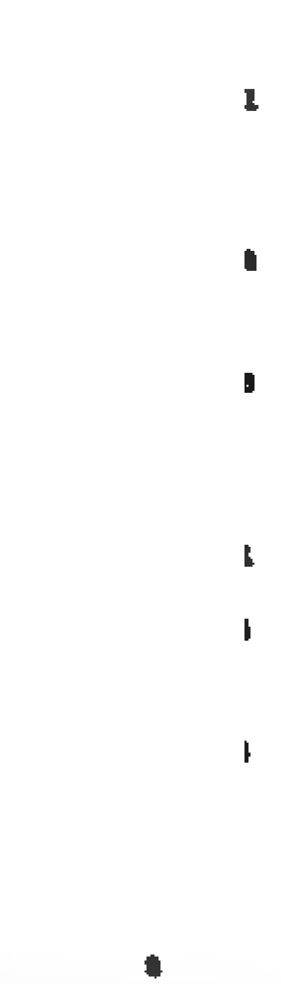
The external granule-layer is composed of large granules, looking like cells, which are each nearly filled with a single nucleus. These are connected with the filaments from the rods and cones. They are rounded or ovoid, and measure from $\frac{1}{12000}$ to $\frac{1}{6000}$ of an inch in diameter. The inter-granule layer (cone-fibre plexus) is composed apparently of minute fibrillæ and a few nuclei. The internal granule-layer is composed of cells nearly like those of the external granule-layer, but a little larger, and probably connected with the filaments of the rods and cones. The granular (molecular) layer is situated next the layer of ganglion-cells.

The layer of ganglion-cells is composed of multipolar

[1] SCHULTZE, *Zur Anatomie und Physiologie der Retina*, Bonn, 1866, S. 52.

cells, like those in the brain, measuring from $\frac{1}{3000}$ to $\frac{1}{750}$ of an inch in diameter. In the centre of the retina, at the macula lutea, the cells present eight layers, and they diminish to a single layer near the periphery. The smaller cells are situated near the centre, and the larger, near the periphery. Each cell sends off several filaments (from two to twenty-five) probably going to the layer of rods and cones, and a single filament, which becomes continuous with one of the filaments of the optic nerve.

FIG. 3.



Perpendicular section of the human retina, made six lines anterior to the entrance of the optic nerve, magnified 350 times.—1, bacillar layer; 2, external granule-layer; 3, intergranule layer (cone-fibre plexus); 4, internal granule-layer; 5, finely granular gray layer; 6, layer of nerve-cells; 7, fibres of the optic nerve; 8, the membrana limitans. (KÖLLIKER, *Manual of Human Microscopic Anatomy*, London, 1860, p. 658.)

The layer formed by the expansion of the optic nerve is composed of pale, transparent nerve-fibres, from $\frac{1}{50000}$ to $\frac{1}{30000}$ of an inch in diameter. These do not call for special description.

The limitary membrane is a delicate structure, with fine striæ and nuclei, composed of connective-tissue elements. It is about $\frac{1}{24000}$ of an inch in thickness. From this membrane, connective-tissue elements are sent into the various layers of the retina, and form a framework for the support of the other structures.[1]

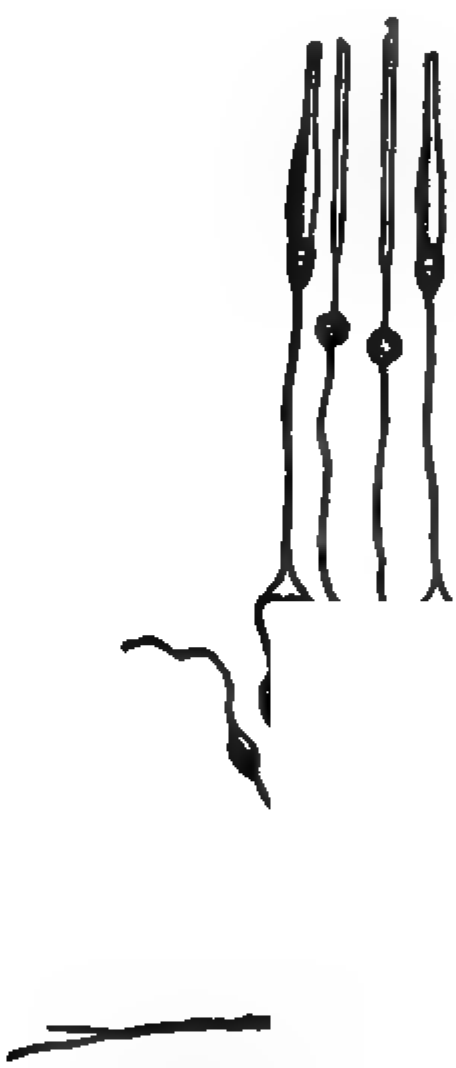
As before remarked, the retina becomes progressively thinner from the centre to the periphery. The granular layers and the nervous layers are rapidly lost in the anterior half of the membrane.

The connection between the rods and cones and the ganglion-cells may be

[1] It is only of late years that the connective-tissue elements of the retina have been accurately recognized. Formerly, much confusion existed because these elements were confounded with the elements of true nerve-tissue. The fibres of Müller undoubtedly belong to connective tissue.

readily understood if we accept the following explanation: The filaments from the bases of the rods and cones pass inward, presenting, in their course, the corpuscles which we have described in the granule-layers, and finally become, as is thought, directly continuous with the poles of the ganglion-cells. The cells, in their turn, each send one filament to the layer formed by the expansion of the optic nerve, which is continuous with a nerve-fibre. This arrangement is shown in Fig. 4.

Fig. 4.



Scheme of the connection of the rods and cones with the true nervous elements of the retina. (Kölliker, *Handbuch der Gewebelehre*, Leipzig, 1867, S. 684.)

The arteries of the retina branch from the arteria centralis, presenting a beautifully arborescent appearance when viewed with the ophthalmoscope. They pass into the layer of gray nervous matter and send their branches to the periphery, where they supply a wide plexus of very small capillaries in the ora serrata. The capillaries empty into an incomplete venous circle, branches from which pass back by the sides of the arteries to the vena centralis. The macula lutea is provided with a rich plexus of minute capillaries.

Crystalline Lens.—The anatomy of the crystalline lens, as far as it bears upon the physiology of vision, is very simple. It is a double-convex lens, transparent, and exceedingly elastic. It has a function in the refraction of the rays of

light analogous to the action of convex lenses in optical instruments. When we come to study its exact structure, however, there are many points that are still undetermined and somewhat obscure; but, fortunately, these are not, as far as we now know, of much physiological importance. In treating of the anatomy of the lens, we shall simply describe the most prominent and the well-determined points in its structure. A complete account of the arrangement of its component parts would necessitate very full and minute descriptions, which could only be elucidated by numerous illustrative figures.

The lens is situated behind the pupil, in what is called the hyaloid fossa of the vitreous humor, which is exactly moulded to its posterior convexity. In the fœtus, the capsule of the lens receives a branch from the arteria centralis; but it is non-vascular in the adult. The anterior convexity is just behind the iris, and the borders are in relation with what is known as the suspensory ligament. The convexities do not present regular curves, and they are so subject to variations after death that the measurements, post mortem, are of little value. During life, however, they have been measured very exactly in the various conditions of accommodation. These measurements will be discussed fully in connection with the physiology of the lens.

The diameters of the lens in the adult are about $\frac{1}{3}$ of an inch transversely and $\frac{1}{4}$ of an inch antero-posteriorly. The convexity is greater on its posterior than on its anterior surface. The form is sufficiently well indicated in Fig. 5 (p. 67) accompanying our summary of the anatomy of the eye. In fœtal life, the convexities of the lens are much greater than in the adult, and its structure is much softer. In old age, the convexities are diminished and the lens becomes harder and quite inelastic, which accounts for the progressive diminution in the power of accommodation.

The important physiological points in the structure of the lens are that it presents an investing membrane, the capsule,

the lens itself being composed of layers of fibres of different degrees of density.

The capsule of the lens is an exceedingly thin, transparent membrane, very elastic, so that when it is torn, the force of its contraction frequently expels its contents. This membrane is generally from $\frac{1}{2400}$ to $\frac{1}{1500}$ of an inch thick; but it is very thin at the periphery, measuring here only $\frac{1}{6000}$ of an inch. Its thickness is increased in old age. On the anterior portion, the capsule is lined with a layer of exceedingly delicate, nucleated epithelial cells. These are situated on the inner surface of the membrane. The posterior half of the capsule has no epithelial lining. The cells are regularly polygonal, from $\frac{1}{2000}$ to $\frac{1}{1200}$ of an inch in diameter, with large, round nuclei. After death they are said to break down into a liquid, known as the liquid of Morgagni, though by some this liquid is supposed to be exuded from the substance of the lens. At all events, the cells disappear soon after death.

If the lens be viewed entire with a low magnifying power, it presents, upon either of its surfaces, a star with from nine to sixteen radiations extending from the centre to about half or two-thirds of the distance to the periphery. The stars seen upon the two surfaces are not coincident, the rays of one being situated between the rays of the other. In the fœtus, the stars are more simple, presenting only three radiations upon either surface. These stars are not fibrous, like the rest of the lens, but are composed of a homogeneous substance, which extends, also, between the fibres.

The greatest part of the substance of the lens is composed of very delicate, soft, and pliable fibres, which are transparent, but perfectly distinct. These fibres are flattened, six-sided prisms, closely packed together, so that their transverse section presents a regularly-tesselated appearance. They are from $\frac{1}{4800}$ to $\frac{1}{2400}$ of an inch broad and from $\frac{1}{13000}$ to $\frac{1}{9000}$ of an inch in thickness. Their flat surfaces are parallel with the surface of the lens. The direction of the fibres is from the centre and from the rays of the stellate figures to the

periphery, where they turn and pass to the star upon the opposite side. The outer layers of fibres, near the equator, or circumference of the lens, are provided with beautifully-distinct, oval nuclei, with one or two nucleoli. These become smaller as we pass deeper into the substance of the lens, and gradually disappear.

The regular arrangement of the fibres of the lens makes it possible to separate its substance into layers, which have been compared by anatomists to the layers of an onion; but this separation is entirely artificial, and the number of apparent layers depends upon the dexterity of the manipulator. It is to be noted, however, that the external portions of the lens are soft, even gelatinous, and that the central layers are much harder, forming a sort of central kernel, or nucleus.

The lens is composed of a peculiar organic nitrogenized substance, very analogous to globuline, called crystalline, combined with various inorganic salts. One of the peculiar constituents of this body is cholesterine. In an examination of four fresh crystalline lenses of the ox, we found cholesterine, in the proportion of 0·907 of a part per 1,000.[1] In some cases of cataract, cholesterine exists in the lens in a crystalline form; but, under normal conditions, it is united with the other constituents.

Suspensory Ligament of the Lens (*Zone of Zinn*).—When we come to the description of the vitreous humor, we shall see that it occupies about the posterior two-thirds of the globe, and is enveloped in a delicate capsule, called the hyaloid membrane. In the region of the ora serrata of the retina, this membrane divides into two layers. The posterior layer lines the depression in the vitreous humor into which the lens is received. The anterior layer passes forward toward the lens, and divides into two secondary layers, one of which

[1] FLINT, JR., *Experimental Researches into a New Excretory Function of the Liver.*—*American Journal of the Medical Sciences*, Philadelphia, 1862, New Series, vol. xliv., p. 313; and, *Recherches expérimentales*, etc., Paris, 1868, p. 18

passes forward to become continuous with the anterior portion of the capsule of the lens, while the other passes to the posterior surface of the lens to become continuous with this portion of its capsule. The anterior of these layers is corrugated, or thrown into folds which correspond with the ciliary processes, with which it is in contact. This corrugated portion is called the zone of Zinn. The two layers thus surround the lens and are properly called its suspensory ligament. As the two layers of the suspensory ligament separate at a certain distance from the lens, one passing to the anterior and the other to the posterior portion of the capsule, there remains a triangular canal, about $\frac{1}{10}$ of an inch wide, surrounding the border of the lens, called the canal of Petit. Under natural conditions, the walls of this canal are nearly in apposition and it contains a very small quantity of clear liquid.

As we have already remarked in describing the retina, at the ora serrata, the membrane is closely connected, by a mutual interlacement of fibres, with the suspensory ligament. It is important to appreciate clearly the relations of the suspensory ligament, in order to understand the mechanism of accommodation of the lens to vision at different distances. The ciliary muscle being in repose, during what is termed the indolent condition of the eye, when it is adapted to vision at long distances, the tension of the parts flattens the lens; but, in the effort of accommodation for near objects, the ciliary muscle contracts, compresses the contents of the globe, relaxes the suspensory ligament, and the inherent elasticity of the lens renders it more convex. It is by a delicate use of this muscle, that the proper adaptation of the curvatures of the lens is obtained.

The membrane forming the suspensory ligament is composed of pale longitudinal and transverse fibres of rather a peculiar appearance, which are much less affected by acetic acid than the ordinary fibres of connective tissue.

Aqueous Humor.—The space bounded in front by the cor-

nea, posteriorly by the crystalline lens and the anterior face of its suspensory ligament, and, at its circumference, by the tips of the ciliary processes, is known as the aqueous chamber. This contains a clear liquid, called the aqueous humor. The iris separates this space into two divisions, which communicate with each other through the pupil; viz., the anterior chamber, situated between the anterior face of the iris and the cornea, and the posterior chamber, between the posterior face of the iris and the crystalline. It is evident, from the position of the iris, that the anterior chamber is much the larger; and, indeed, the posterior surface of the iris and the anterior surface of the lens are in contact, except, perhaps, near their periphery or when the iris is very much dilated. The liquid filling the chambers of the eye is said to be secreted by the blood-vessels of the ciliary processes; at all events, it is rapidly reproduced after it has been evacuated, as occurs in many surgical operations on the eye.

There is very little to be said concerning the properties and composition of the aqueous humor. It is perfectly colorless and transparent, faintly alkaline, of a specific gravity of about 1,005, and possesses the same index of refraction as the cornea and the vitreous humor. As we should infer from its low specific gravity, the aqueous humor is composed chiefly of water. It contains a small quantity of an albuminoid matter, but is not rendered turbid by heat or other agents which coagulate albumen. Various inorganic salts, the chlorides, sulphates, phosphates, and carbonates, exist in this liquid, in small proportion. It contains also traces of urea and glucose.

Vitreous Humor.—The vitreous humor is a clear, glassy substance, occupying about the posterior two-thirds of the globe. It is enveloped in an exceedingly delicate, structureless capsule, called the hyaloid membrane, which is about $\frac{1}{5000}$ of an inch in thickness. This membrane adheres pretty strongly to the limitary membrane of the retina. In front,

at the ora serrata, as we have already seen, the hyaloid membrane is thickened, and becomes continuous with the suspensory ligament of the lens.

The vitreous humor itself is gelatinous, of feeble consistence, slightly alkaline in its reaction, with a specific gravity of about 1,005. Upon section, there oozes from it a watery fluid of a slightly mucilaginous consistence. This humor is not affected by heat or alcohol, but is coagulated by certain mineral salts, more especially the acetate of lead. When thus solidified, it presents regular layers, like the white of an egg boiled in its shell; but these are artificial. In the embryon, the vitreous humor is divided into numerous little cavities, and contains cells and leucocytes. It is also penetrated by a branch from the central artery of the retina, which passes through its centre to ramify on the posterior surface of the crystalline lens. This structure, however, is not found in the adult, the vitreous humor being then entirely without blood-vessels.

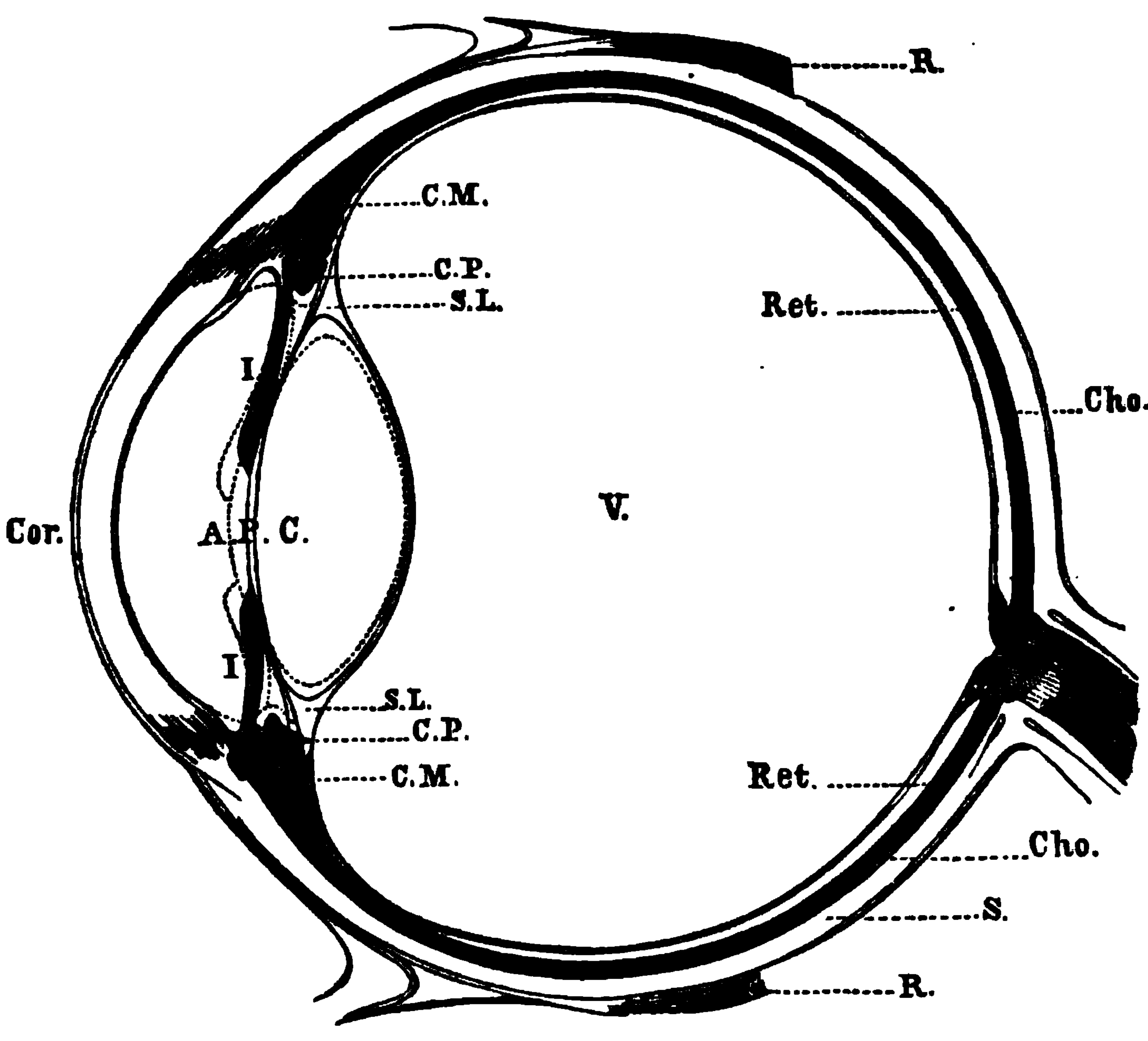
There is still considerable difference of opinion with regard to the structure of the vitreous humor in the adult; some anatomists believing that it is perfectly homogeneous and that the so-called laminæ are produced only by the action of reagents, while others state that it is divided into compartments, by processes penetrating from and connected with the hyaloid membrane. The weight of authority is decidedly in favor of a subdivision of the humor into compartments formed by delicate membranes radiating from the point of penetration of the optic nerve to the anterior boundary where the hyaloid membrane is in contact with the capsule of the lens. In this way, the humor is divided up, something like the half of an orange, by about one hundred and eighty membranous processes of extreme delicacy, which do not interfere with its transparency.

Summary of the Anatomy of the Globe of the Eye.

For the intimate structure of the various coats of the eye,

their dimensions, etc., the reader is referred to the descriptions just given of these parts. In this summary, we propose simply to show the relations of the various parts, giving, at the same time, a brief statement of their physiological importance. This end will be attained by a full explanation of Fig. 5, which represents a section of the human eye, and shows the relations of its various coats, humors, etc.

FIG. 5.



Section of the human eye, taken from Helmholtz, and slightly modified. (*Revue des cours scientifiques*, Paris, 1868-1869, tome vi., p. 215.)

The eyeball is nearly spherical in its posterior five-sixths, its anterior sixth being formed of the segment of a smaller sphere, which is slightly projecting. The posterior five-sixths presents the following coats, indicated in the figure:

S. The sclerotic; a dense, fibrous membrane, chiefly for the protection of the more delicate structures of the globe, and giving attachment to the muscles which move the eyeball. Attached to the sclerotic, are the tendons of R, the recti muscles.

Cor. The cornea; a transparent structure, forming the anterior, projecting sixth of the globe; dense and resisting, allowing, however, the passage of light; covered, on its convex surface, with several layers of transparent epithelial cells, and, on its posterior surface, with the membrane of the aqueous humor.

Cho. The choroid coat, lining the sclerotic and extending only as far forward as the cornea; connected with the sclerotic by loose connective tissue, in which ramify blood-vessels and nerves, and presenting an external, vascular layer and an internal, pigmentary layer, which latter gives its characteristic dark-brown color.

C. P. The ciliary processes; peculiar folds of the choroid, which form its anterior border, and which embrace the folds of the suspensory ligament of the lens.

C. M. The ciliary muscle, formerly called the ciliary ligament; a muscular ring, situated just outside of the ciliary processes, arising from the circular line of junction of the sclerotic with the cornea, and passing over the ciliary processes, to become lost in the fibrous tissue of the choroid. This is sometimes called the tensor of the choroid. Its action is to tighten the choroid over the vitreous humor, relax the ciliary processes and the suspensory ligament of the lens, when the lens, by virtue of its elasticity, becomes more convex. The ciliary muscle is the active agent in accommodation. In the figure, the mechanism of accommodation is shown by the dotted lines, which represent the suspensory ligament relaxed by the contraction of the ciliary muscle, and the lens, increased in its convexity, pushing forward the iris.

I. The iris; dividing the space in front of the lens into two chambers occupied by the aqueous humor: (A) The an-

terior chamber is much the larger. The iris, in its central portion surrounding the pupil (P), is in contact with the lens. Its circumference is just in front of the line of origin of the ciliary muscle.

Ret. The retina; an exceedingly delicate, transparent membrane, lining the choroid and extending to about $\frac{1}{18}$ of an inch behind the ciliary processes, the anterior margin forming the ora serrata. O. The optic nerve penetrating the retina a little internal to and below the antero-posterior axis. The layer of rods and cones is situatcd externally, next the choroid. Internal to the layer of rods and cones, are the four granular layers; next, the layer of nerve-cells; next, the expansion of the fibres of the optic nerve; and next, in apposition with the hyaloid membrane of the vitreous humor, is the limitary membrane. The layer of rods and cones is supposed to be the portion which receives visual impressions, the rods and cones being connected with the nerve-cells, and through them with the fibres of the optic nerve, by delicate filaments. The macula lutea and the fovea centralis are exactly in the axis of vision.

C. The crystalline lens; elastic, transparent, enveloped in its capsule and surrounded by S. L., the suspensory ligament.

S. L. The suspensory ligament; the anterior layer connected with the anterior portion of the capsule of the lens, and the posterior, with the posterior portion of the capsule. The folded portion of this ligament, which is received between the folds of the ciliary processes, is called the zone of Zinn. The triangular canal between the anterior and the posterior layers of the suspensory ligament and surrounding the equator of the lens is called the canal of Petit.

V. The vitreous humor; enveloped in the structureless hyaloid membrane, which membrane is continuous in front with the suspensory ligament of the lens.

CHAPTER IV.

REFRACTION IN THE EYE.

The eye as an optical instrument—Laws of refraction, dispersion, etc., bearing upon the physiology of vision—Angle alpha—Theories of light—Theories of colors—Color-blindness—Refraction by lenses—Myopia and hypermetropia—Spherical aberration—Chromatic aberration—Formation of images in the eye—Area of distinct vision—Punctum cæcum—Mechanism of refraction in the eye—Refraction by the cornea—Refraction by the crystalline lens—Simple, schematic eye—Astigmatism.

It is simply impossible to obtain a clear idea of the physiology of vision without having carefully studied the physiological anatomy of the visual organs; and, for this reason, we have been as exact as possible and somewhat minute in our description of the structure of the eye. If the student will carefully study the anatomy of the parts, a very succinct statement of some of the well-established laws of refraction will render the physiology so simple that it will follow almost without explanation.

In applying the laws of the refraction of light to the transparent media of the eye, it is necessary to bear in mind certain general facts with regard to vision, that have as yet been referred to either very briefly or not at all.

The eye is not by any means a perfect optical instrument, looking at it from a purely physical point of view. This statement, however, should not be understood as implying that the arrangement of the organs of vision is not such as to adapt them perfectly to the functions which they have to perform in connection with the proper appreciation of visual impressions. By physical tests, it can be demonstrated that the eye is not entirely achromatic; but, in ordinary vision, the

dispersion of colors is not appreciated.[1] There is but a single point in the retina, the fovea centralis, where vision is absolutely distinct; and it is upon this point that images are made to fall when the eye is directed toward any particular object.

It is curious to note, however, that the refracting apparatus is not exactly centred, a condition so essential to the satisfactory performance of our most perfect optical instruments. For example, in a compound microscope or a telescope, the centres of the different lenses entering into the construction of the instrument are all situated in a straight line. Were the eye a perfect optical instrument, the line of vision would coincide exactly with the axis of the cornea; but this is not the case. The visual line (a line drawn from an object to its image on the fovea centralis) deviates from the axis of the cornea, in normal eyes, to the nasal side. The visual line, therefore, forms an angle with the axis of the cornea; and this is known as the angle alpha. This deviation of the visual line from the mathematical centre of the eye is observed both in the horizontal and in the vertical planes. "The horizontal deviation varies from two to eight degrees (*Schuerman*), the vertical, from one to three degrees (*Mandelstamm*)."[2] Of course, this want of exact centration of the optical apparatus, in normal eyes, does not practically affect distinct vision, for, when the eyes are directed toward any object, this object is brought in the line of the visual axis; but the angle alpha is an important element to be taken into account in various mathematical calculations connected with the physics of the eye.

The field, or area of distinct vision, is quite restricted; but, were it larger, it is probable that the mind would become confused with the extent and variety of the impressions, and that we should be unable so easily to observe minute details and fix the attention upon small objects.

[1] HELMHOLTZ, *Optique physiologique*, Paris, 1867, p. 173.

[2] STELLWAG VON CARION, *Treatise on the Diseases of the Eye*, New York, 1868, p. 569.

While we see certain objects with absolute distinctness in a restricted field, the angle of vision is very wide, and rays of light are admitted from an area equal nearly to the half of a sphere. Such a provision is eminently well adapted to our requirements. We direct the eyes to a particular point and see a certain object distinctly, getting the advantage of an image in the two eyes exactly at the points of distinct vision; the rays coming from without the area of distinct vision are received upon different portions of the surface of the retina and produce an impression more or less indistinct, not interfering with the observation of the particular object to which the attention is for the moment directed; but even while looking intently at any object, the attention may be attracted by another object of an unusual character, which might, for example, convey an idea of danger, and the point of distinct vision can be turned in its direction. Thus, while we see distinctly but few objects at one time, the area of indistinct vision is immense; and our attention may be readily directed to unexpected or unusual objects that may come within any portion of the field of view. The small extent of the area of distinct vision, especially for near objects, may be readily appreciated if we watch a person attentively reading a book, when the eyes will be seen to follow the lines from one side of the page to the other with perfect regularity. When we consider that, in addition to these remarkable qualities, which are never thought of in artificial optical instruments, the eye may be accommodated at will, with the most exquisite nicety, to vision at different distances, and that we possess correct appreciation of form, etc., by the use of the two eyes, it is evident that the organ of vision gains rather than loses in comparison with the most perfect instruments that ever have been, or probably ever will be constructed.

Laws of Refraction, Dispersion, etc., bearing upon the Physiology of Vision.

In the present state of physiological science, we have lit-

tle to do with the theory of light, except as regards the modifications of luminous rays in passing through the refracting media of the eye. It will be sufficient to state that nearly all physicists of the present day agree in accepting what is known as the theory of undulation, rejecting *in toto* the emission-theory proposed by Newton. Newton supposed that all luminous bodies gave off inconceivably small particles capable of traversing space with wonderful rapidity and of penetrating transparent bodies. This view was at first very generally accepted; but, as scientific facts accumulated, it was found to be opposed to many optical phenomena, and the theory of undulation now takes its place. It is necessary to the theory of undulation to assume that all space and all transparent bodies are permeated with what has been called a luminiferous ether; and that light is propagated by a vibration or undulation of this hypothetical substance. This theory assimilates light to sound, in the mechanism of its propagation; but, in sound, the waves are supposed to be longitudinal, or to follow the line of propagation, while in light the particles are supposed to vibrate transversely, or at right angles to the line of propagation. It must be remembered, however, that the undulatory theory of sound is capable of positive demonstration, and that the propagation of sound by waves can only take place through ponderable matter, the vibrations of which can always be observed; while luminous vibrations involve the existence of an imponderable and purely hypothetical ether. It is possible, indeed, that scientific facts may, in the future, render the existence of such an ether improbable or its supposition unnecessary; but, at present, all we can say is that the theory of luminous undulation is entirely in accord with the optical phenomena that have thus far been recognized.

The different calculations of physicists with regard to the velocity of light have been remarkably uniform in their results. The lowest calculations put it at about 185,000 miles in a second, and the highest, at about 195,000 miles. The

rate of propagation is usually assumed to be about 192,000 miles.

The intensity of light is in proportion to the amplitude of the vibrations. The intensity diminishes as the distance of the luminous body increases, and is in inverse ratio to the square of the distance.

In the theory of the colors into which pure white light may be decomposed by prisms, it is assumed, as a matter of demonstration, that the waves of the different colors of the solar spectrum are not of the same length. The decomposition of light is produced by differences in the refrangibility of the different colored rays as they pass through a denser medium than the air. The differences in the wave-lengths for different colors is very simply set forth by Tyndall as follows:

"The color of light is determined solely by its wave-length. The ether-waves gradually diminish in length from the red to the violet. The length of a wave of red light is about $\frac{1}{39000}$ of an inch; that of the wave of violet light is about $\frac{1}{57500}$ of an inch. The waves which produce the other colors of the spectrum lie between these extremes.

"The velocity of light being 192,000 miles in a second, if we multiply this number by 39,000, we obtain the number of waves of red light in 192,000 miles; the product is 474,439,680,000,000. All of these waves enter the eye in a second. In the same interval 699,000,000,000,000 waves of violet light enter the eye. At this prodigious rate is the retina hit by the waves of light.

"Color, in fact, is to light, what pitch is to sound. The pitch of a note depends solely on the number of aërial waves which strike the ear in a second. The color of light depends on the number of ethereal waves which strike the eye in a second. Thus the sensation of red is produced by imparting to the optic nerve four hundred and seventy-four millions of millions of impulses per second, while the sensation of violet is produced by imparting to the nerve six hundred and ninety-

nine millions of millions per second."[1] In this way the scale of colors in the solar spectrum is compared to the scale of musical notes and intervals. Indeed, Helmholtz has constructed a theoretical scale of colors to correspond with musical tones and semitones.[2]

The analysis of white light into the different colors of the spectrum shows that it is compound; and, by synthesis, the colored rays may again be brought together, producing white light. Colors may be obtained by decomposition of light by transparent bodies, the different colored rays being refracted, or bent by a prism at different angles. It is not in this way, however, that the colors of different objects are produced. Certain objects have the property of reflecting the rays of light. A perfectly smooth, polished surface, like a mirror, may reflect all of the rays; and the object then has no color, only the reflected light being appreciated by the eye. Certain other objects do not reflect all of the rays of light, some of them being lost to view, or absorbed. When an object absorbs all of the rays, it has no color, and is called black. When an object absorbs the rays equally, and reflects a portion of these rays without decomposition, it is gray or white. There are many objects, however, that decompose white light, absorbing certain rays of the spectrum and reflecting others. The rays not absorbed, but returned to the eye by reflection, give color to the object. Thus, if an object absorb all of the rays of the spectrum except the red, the red rays strike the eye, and the color of the object is red. So it is with objects of different shades, the colors of which are given simply by the unabsorbed rays.

It is a curious fact that the mixture of different colors in certain proportions will result in white. Two colors, which, when mixed, result in white, are called complementary. The following colors of the spectrum bear such a relation to each other:

[1] TYNDALL, *Light and Electricity*, New York, 1871, p. 65.

[2] HELMHOLTZ, *Optique physiologique*, Paris, 1867, p. 319.

Red and greenish-blue.
Orange and cyanogen-blue.
Yellow and indigo-blue.
Greenish-yellow and violet.[1]

The fact that impressions made upon the retina persist for an appreciable length of time enables us to illustrate the law of complementary colors. If a disk, presenting divisions with two complementary colors, be made to revolve so rapidly that the impressions made by the two colors are blended, the resulting color is white.

It is almost useless, with our present knowledge, to speculate with regard to the probable mechanism of the appreciation of colors in vision. The facts just stated are sufficiently clear, showing that the number of ethereal vibrations is different for different colors; but it is by no means determined that differences in the amplitude of the vibrations are in direct relation with the arrangement of the disks of the rods and cones in different portions of the retina.[2] The curious phenomena of color-blindness depend upon an abnormal condition of the visual apparatus. Persons possessing this peculiarity—called sometimes Daltonism, after the celebrated English chemist, who described this infirmity as it existed in his own person—though vision may be normal in other re-

[1] TYNDALL, *Light and Electricity*, New York, 1871, p. 70.

[2] ZENKER, *Versuch einer Theorie der Farben-Perception.—Archiv für mikroskopische Anatomie*, Bonn, 1867, Bd. iii., S. 248, *et seq.* In this article, Zenker proposes the theory of the perception of colors referred to above; but, as far as we know, this has not been unreservedly adopted by any writers upon physiological optics, though it must be admitted to be the only theory of color-perception that approaches a satisfactory explanation of this most difficult question. We are by no means prepared to deny *in toto* the proposition that the perception of color is a question of situation, different colors being appreciated by different portions of the retina; and some of the facts with relation to color-blindness are favorable to this view; still, to render this certain, it is necessary to establish a very exact relation between the length of the waves of light of different colors and the diameter and number of the disks of the sensitive elements of the retina. For a very fair and full discussion of this theory, the reader is referred to the admirable compendium of Kaiser. (*Compendium der physiologischen Optik*, Wiesbaden, 1872, S. 151, *et seq.*)

spects, cannot distinguish certain colors, will mistake red for green, etc., and some can only distinguish black and white. It is a curious fact, also, that persons affected with color-blindness (Daltonism, achromatopsia) are sometimes incapable of discriminating musical tones. This was noted in numerous instances by Dr. Pliny Earle.[1] Though often congenital and irremediable, it is now known that color-blindness is sometimes produced by the excessive use of alcohol and tobacco, exposure to cold and wet, etc., and is amenable to treatment.[2]

Refraction by Lenses.—A ray of light is an imaginary pencil, so small as to present but a single line; and the light admitted to the interior of the eye by the pupil is supposed to consist of an infinite number of such rays. In studying the physiology of vision, it is important to recognize the laws of refraction of rays by the transparent bodies bounded by curved surfaces, with particular reference to the action of the crystalline lens.

The action of a double-convex lens, like the crystalline, in the refraction of light, may be readily understood if we simply apply the well-known laws of refraction by prisms. A ray of light falling upon the side of a prism at an angle is deviated toward a line perpendicular to the surface of the prism. As the ray passes from the prism to the air, it is again refracted, but then the deviation is from the perpendicular of the second surface of the prism. If we imagine two prisms placed together, as in Fig. 6, the ray A B will be bent toward the perpendicular G B to M. As it passes from the prism, it will be refracted from the perpendicular H M and take the direction M I. Corresponding refraction takes place in the ray N O falling upon the lower prism. These two rays will cross each other at the point L.

[1] EARLE, *On the Inability to distinguish Colours.—American Journal of the Medical Sciences*, Philadelphia, 1845, New Series, vol. ix., p. 351.

[2] DERBY, *Color-blindness, and its Acquisition through the Abuse of Alcohol and Tobacco.—New York Medical Journal*, 1871, vol. xiii., p. 284, *et seq.*

A circle is supposed to be equivalent to a polygon with an infinite number of sides. A regular double-convex lens is a transparent body bounded by portions of a sphere, and may

Fig. 6.

be assumed to be composed of an infinite number of prisms. The action of a convex lens is to converge the rays of light

Fig. 7.

falling upon different portions of their surface so that they cross at a certain distance behind the lens. If we imagine the lens A B (Fig. 7) to be free from spherical aberration,

the rays C D and C E, from the point C, will be refracted and brought to a focus at the point F. In the same way, the rays from the point K will be brought to a focus at the point L, the two sets of rays crossing at G. The same is true for all of the rays from the object C K, which strike the lens at an angle; but the ray H I, which is perpendicular to the lens, is not deviated. The line H I is called the axis of the lens. These facts may be applied to the crystalline lens. The rays from an object C K fall upon the lens and are brought to a focus so as to produce the image L F. The retina is supposed to be at such a distance from the lens that the rays are brought to a focus exactly at its surface. Inasmuch as the rays cross each other at the point G, the image is always inverted.

Supposing the crystalline lens to be free from spherical and chromatic aberration, the formation of a perfect image depends upon the following conditions:

The object must be at a certain distance from the lens. If the object be too near, the rays, as they strike the lens, are too divergent, and are brought to a focus beyond the plane L I F, or behind the retina; and, as a consequence, the image is confused. In optical instruments, the adjustment is made for objects at different distances by moving the lens itself. In the eye, however, the adjustment is effected by increasing or diminishing the curvatures of the lens, so that the rays are always brought to a focus at the visual surface of the retina. The faculty of thus changing the curvatures of the crystalline lens is called accommodation. This power, however, is restricted within certain well-defined limits.

In some individuals, the antero-posterior diameter of the eye is too long, and the rays, for most objects, come to a focus before they reach the retina. This defect may be remedied by placing the object very near the eye, so as to increase the divergence of the rays as they strike the crystalline. Such persons are said to be near-sighted (myopic), and objects are

only seen distinctly when very near the eye. This defect may be remedied for distant objects by placing concave lenses before the eyes, by which the rays falling upon the crystalline are diverged. The opposite condition, in which the antero-posterior diameter is too short (hypermetropia), is such that the rays are brought to a focus behind the retina. This is corrected by converging the rays of incidence by placing convex lenses before the eyes. In old age, the crystalline lens becomes flattened, its elasticity is diminished, and the power of accommodation is lessened; conditions which also tend to bring the rays to a focus behind the retina. This condition is called presbyopia. To render near vision, as in reading, distinct, objects are placed farther from the eye than under normal conditions. The defect may be remedied, as in hypermetropia, by placing convex lenses before the eyes, by which the rays are converged before they fall upon the crystalline lens.

The mechanism of accommodation will be fully considered in connection with the physiology of the crystalline lens; at present, it is sufficient to state that, in looking at distant objects, the rays, as they fall upon the lens, are nearly parallel. The lens is then in repose, or "indolent." It is only when an effort is made to see near objects distinctly, that the agents of accommodation are called into action; and then, very slight changes in the curvature of the lens are sufficient to bring the rays to a focus exactly on the visual surface of the retina.

Spherical Aberration.—In a convex lens, with its surfaces consisting of portions of a perfect sphere, the rays of light from any object are not converged to a uniform focus, and the production of an absolutely distinct image is impossible. For example, if we suppose the crystalline lens to present regular curvatures, the rays refracted by its peripheral portion would be brought to a focus in front of the retina; the focus of the rays converged by the lens near its centre would be behind

the retina; a few, only, of the rays would have their focus at the retina itself; and, as a consequence, the image would appear confused. This is illustrated in imperfectly-corrected lenses, and is called spherical aberration. For example, in examining an object with an imperfectly-corrected objective under the microscope, it is evident that the field of view is not uniform, and that there is a different focal adjustment for the central and the peripheral portions of the lens. In the construction of optical instruments, this difficulty may be in part corrected if the rays of light be cut off from the periphery of the lens by a diaphragm, which is an opaque screen with a circular perforation allowing the rays to pass to a restricted portion of the lens near its centre. The iris corresponds to the diaphragm of optical instruments, and corrects the spherical aberration of the crystalline in part, by eliminating a portion of the rays that would otherwise fall upon its peripheral portion. But this correction is not sufficient for high magnifying powers; and it is only by the more or less perfect correction of this kind of aberration by other means, that powerful lenses have been rendered available in optics.

The spherical aberration of lenses which diverge the rays of light is precisely opposite to the aberration of converging lenses. If, therefore, we construct a compound lens, it is possible to fulfil the conditions necessary to the convergence of all the incident rays to a focus on a uniform plane, so that the image produced behind the lens is not distorted. Given, for example, a double-convex lens, by which the rays are brought to innumerable focal points situated in different planes. The fact that but a few of these focal points are in the plane of the retina renders the image indistinct. If we place behind this convex lens a concave lens, by the action of which the rays are more or less diverged, the inequality of the divergence by different portions of the second lens will have the following effect: As the angle of divergence gradually increases from the centre toward the periphery,

the rays near the periphery, which are most powerfully converged by the convex lens, will be most widely diverged by the peripheral portion of the concave lens; so that, if the opposite curvatures be accurately adjusted, the aberrant rays may be blended. It is evident that, if all of the rays were equally converged by the convex lens and equally diverged by the concave lens, the action of the latter would be simply to elongate the focal distance; and it is equally evident that, if the aberration of the one be exactly opposite to the aberration of the other, there will be perfect correction. Mechanical art has not enabled us to effect correction of every portion of very powerful convex lenses in this way; but, by a combination of lenses and diaphragms together, highly-magnified images, nearly perfect, have been produced.

It is evident that, for distinct vision at different distances, the crystalline lens must be nearly free from spherical aberration. This is not effected by a combination of lenses, as in ordinary optical instruments, but by the curvatures of the lens itself, and by certain differences in the consistence of different portions of the lens, which will be fully considered hereafter.

Chromatic Aberration.—We have already alluded to the fact that a refracting medium does not act equally upon the different colored rays into which pure white light may be decomposed; in other words, as the pure ray falling upon the inclined surface of a glass prism is bent, it is decomposed into the colors of the spectrum. As a convex lens is practically composed of an infinite number of prisms, the same effect would be expected. Indeed, a simple convex lens, even if the spherical aberration be corrected, always produces more or less decomposition of the light. The image formed by such a lens will consequently be colored; and this defect in simple lenses is called chromatic aberration. At the same time, it is evident that the centre of the different rays from an object will be composed of all the colors of the spectrum combined, producing the effect of white light; but, at the

borders, the different colors will be separate and distinct, and an image produced by a simple convex lens will thus be surrounded by a circle of colors, like a rainbow.

In prisms, the chromatic dispersion may be corrected by allowing the colored rays from one prism to fall upon a second prism, which is inverted, so that the colors will be brought together and produce white light. Two prisms thus applied to each other constitute, in fact, a flat plate of glass, and the rays of light pass without deviation. If this law be applied to lenses, it is evident that the dispersive power of a convex lens may be exactly opposite to that of a concave lens. By the convex lens, the colored rays are separated by convergence; while, in the concave lens, the colored rays are dispersed in the opposite direction. If, then, we combine a convex with a concave lens, the white light decomposed by the one will be recomposed by the other, and the chromatic aberration will thus be corrected. But, in using a convex and a concave lens composed of the same material, the convergence by the one will be neutralized by the dispersion of the other, and there will be no amplification of the object.

In the construction of optical instruments, the chromatic aberration is corrected, with but slight diminution in the amplification, by combining lenses made of different material, as of flint-glass and crown-glass. Flint-glass has a much greater dispersive power than crown-glass. If, therefore, we use a convex lens of crown-glass combined with a concave lens of flint-glass, the chromatic aberration of the convex lens may be corrected by a concave lens with a curvature which will take but little from the magnifying power. A compound lens, with the spherical aberration of the convex element corrected by the curvature of a concave lens, and the chromatic aberration corrected by the curvature, in part, and in part by the superior refractive power of flint-glass over crown-glass, will produce a perfect image.

Although the eye is not absolutely achromatic, the dispersion of light is not sufficient to interfere with distinct

vision. We can understand how the chromatic aberration is practically corrected in the crystalline lens, when we remember that its various layers are of different consistence and of different refractive power.

Formation of Images in the Eye.

It is only necessary to call to mind the general arrangement of the different structures in the eye and to apply the simple laws of refraction, to comprehend precisely how images are formed upon the retina.

The eye corresponds to a camera obscura. Its interior is lined with a dark, pigmentary membrane, the choroid, the function of which is to prevent the confusion of images by internal reflection. The rays of light are admitted through a circular opening, the pupil, the size of which is regulated by the movements of the iris. The pupil is contracted when the light striking the eye is intense, and is dilated as the amount of light is diminished. In the accommodation of the eye, the pupil is dilated for distant objects and contracted for near objects; for, in looking at near objects, the aberrations of sphericity and achromatism in the lens are more marked, and the peripheral portion is cut off by the action of this movable diaphragm, thus aiding the correction. The rays of light from an object pass through the cornea, the aqueous humor, the crystalline lens, and the vitreous humor, and are refracted with so little spherical and chromatic aberration that the image formed upon the retina is practically perfect. The layer of rods and cones of the retina is the only portion of the eye endowed directly with special sensibility, the impressions of light being conveyed to the brain by the optic nerves. This layer is situated next the choroid, but the other layers of the retina, through which the light passes to reach the rods and cones, are perfectly transparent.

It has been positively demonstrated that the rods and cones are the only structures capable of directly receiving visual impressions, by the following interesting experiment,

first made by Purkinje:[1] We concentrate upon the sclerotic, with a convex lens of short focus, an intense light, at a point as far as possible removed from the cornea. This passes through the translucent coverings of the eye at this point, and the image of the light reaches the retina. If we then look at a dark surface, we have the field of vision presenting a reddish-yellow illumination, with a dark, arborescent appearance produced by the shadow of the large retinal vessels; and, as we move the lens slightly, the shadow of the vessels moves with it. Without going elaborately into the mechanism of this remarkable phenomenon, it is sufficient to state that Heinrich Müller[2] has arrived at an absolute mathematical demonstration that the shadows of the vessels are formed upon the layer of rods and cones, and that this layer alone is capable of receiving impressions of light. His explanation is accepted by all writers at the present day, and is regarded as positive proof of the peculiar sensibility of this portion of the retina. In carefully-conducted observations of this kind, a spot is seen in which no vessels appear, which corresponds to the fovea centrālis. When the experiment is prolonged, the vessels disappear, as the sensibility of the retina becomes diminished by fatigue.[3]

Theoretically, an illuminated object placed in the angle of vision would form upon the retina an image, diminished in size and inverted. This fact is capable of actual demonstration. In white rabbits and other albinos, Magendie has been able, by removing the fat and muscles covering the posterior portion of the eye, to see the image of a flame upon the retina, inverted and diminished.[4] By an ingeniously-arranged

[1] PURKINJE, *Beiträge zur Kenntniss des Sehens in subjectiver Hinsicht*, Prag, 1819, S. 89, *et seq.*

[2] HEINRICH MÜLLER, *Anatomisch-physiologische Untersuchungen über die Retina*, Leipzig, 1856, S. 107, *et seq.*

[3] HELMHOLTZ, *Optique physiologique*, Paris, 1867, p. 214, *et seq.*

Helmholtz gives a very full explanation of these phenomena and of their physiological importance.

[4] MAGENDIE, *Précis élémentaire de physiologie*, Paris, 1836, tome i., p. 79.

experiment in a dark chamber, Volkmann has observed such an image in the human subject.[1] The most satisfactory observations, however, have been made with the ophthalmoscope. With this instrument, the retina and the images formed upon it may be seen during life with perfect distinctness.[2]

All parts of the retina, except the point of entrance of the optic nerve, are sensible to light; and the arrangement of the cornea and pupil is such, that the field of vision is, at the least estimate, equal to the half of a sphere. If a ray of light fall upon the border of the cornea at a right angle to the axis of the eye, it is refracted by its surface and will pass through the pupil to the border of the retina upon the opposite side. Above and below, the circle of vision is cut off by the overhanging arch of the orbit and the malar prominence; but externally the field is free. With the two eyes, therefore, the lateral field of vision must be equal to at least one hundred and eighty degrees. It is easy to demonstrate, however, by the ophthalmoscope, as well as by taking cognizance of the impressions made by objects far removed from the axis of distinct vision, that images formed upon the lateral and peripheral portions of the retina are confused and imperfect. We have a knowledge of the presence and an indefinite idea of the general form of large objects situated outside of the area of distinct vision; but, when we wish to note such objects exactly, the eyeball is turned by muscular effort, so as to bring them at or very near the axis of the globe. This fact, with what we know of the mechanism of refraction by the cornea and lens, makes it evident that the area of the retina upon which images are formed with perfect distinctness is quite restricted. A moment's reflection is sufficient to convince any one, that, in order to see any object distinctly, we must look at it, or bring the axis of the eye to

[1] VOLKMANN, *Sehen*, in WAGNER, *Handwörterbuch der Physiologie*, Braunschweig, 1846, Bd. iii., Erste Abtheilung, S. 287.

[2] HELMHOLTZ, *Optique physiologique*, Paris, 1867, p. 87.

bear upon it directly. Let us see, now, how far this fact is capable of positive demonstration.

If we examine the bottom of the eye with the ophthalmoscope, we can see the yellow spot with the fovea centralis, apparently free from blood-vessels, and composed, as we know, chiefly of those elements of the retina which are sensitive to light. If, at the same time, we examine an image for which the eye is perfectly adjusted, it will be seen that this image is perfect only at the fovea centralis; and, if the object be removed from the axis of vision, we see a confused image upon the retina removed from the fovea, at the same time that the subject is conscious of indistinct vision. In the words of Helmholtz, "it is only in the immediate vicinity of the ocular axis that the retinal image possesses entire distinctness; beyond this, the contours are less defined. It is in part for this reason that in general we see distinctly in the field of vision, only the point that we fix. All the others are seen vaguely. This lack of distinctness in indirect vision, in addition, depends also upon diminished sensibility of the retina: at a slight distance from the fixed point, the distinctness of vision has diminished much more than the objective distinctness of retinal images."[1]

At the point of penetration of the optic nerve, the retina is insensible to luminous impressions; at least, its sensibility is so obtuse as to be entirely inadequate for the purposes of vision. This point is called the punctum cæcum; and its want of sensibility was demonstrated many years ago by the experiments of Mariotte, which we quote *verbatim:*

"I fasten'd on an obscure Wall about the hight of my Eye, a small round paper, to serve me for a fixed point of Vision; and I fastened such an other on the side thereof towards my right hand, at the distance of about 2. foot; but somewhat lower than the first, to the end that it might strike the *Optick Nerve* of my Right Eye, whilst I kept my Left shut. Then I plac'd myself over against the First paper, and

[1] HELMHOLTZ, *Optique physiologique*, Paris, 1867, p. 88.

drew back by little and little, keeping my Right Eye fixt and very steddy upon the same; and being about 10. foot distant, the second paper totally disappear'd."[1]

In this experiment, the rays of light from the paper which has disappeared from view are received upon the punctum cæcum, at the point of entrance of the optic nerve. If the observer withdraw himself still farther, the second circle will reappear, as the rays are removed from the punctum cæcum. With the ophthalmoscope, the point of penetration of the optic nerve may be readily seen in the living eye. If the image of a flame be directed upon this point, the sensation of light is either not perceived, or it is very faint and indefinite, and is then probably due to diffusion to other portions of the retina.

The relative sensibility of different portions of the retina has been accurately measured by Volkmann, and has been found to be in an inverse ratio equal to about the square of the distance from the axis of most perfect vision. This observer calculated the distance between the sensitive elements of the retina at which he supposed that two parallel lines would appear as one. In the axis of vision, the distance was 0·00029″, and, at a deviation inward of 8°, it was 0·03186″, a diminution of acuteness of more than a hundred times. The following table gives the results of these experiments:

Angle of deviation of the object seen, from the visual axis inward.	Calculated distance, for the retinal elements, of the parallel lines.
0°	0·00029″
1°	0·00055″
2°	0·00091″
3°	0·00141″
4°	0·00153″
5°	0·00180″
6°	0·00383″
7°	0·01527″
8°	0·03186″

[1] MARIOTTE, *A New Discovery touching Vision.—Philosophical Transactions*, London, 1668, vol. iii., p. 668.

This table illustrates, with great exactness, the gradual diminution in the acuteness of vision as the impressions are made farther and farther from the visual axis.[1] The experiments were made upon the same principle as that of observations upon the tactile sensibility of different portions of the skin by testing the power of distinguishing the two points of the æsthesiometer.[2]

The fact of the formation of images upon the retina, which are exact only at or immediately surrounding the fovea centralis, being settled, it remains to see how these images are rendered perfect, and to study the mechanism of refraction by the transparent media of the eye.

Mechanism of Refraction in the Eye.

A visible object sends rays from every point of its surface to the cornea. If the object be near, the rays from each and every point are divergent as they strike the eye. Rays from distant objects are practically parallel. It is evident that the refraction for diverging rays must be greater than for parallel rays, as a necessity of distinct vision; in other words, the eye must be accommodated for vision at different distances. Leaving, however, the mechanism of accommodation for future consideration, we shall endeavor to show how the rays of light as they penetrate the eye are refracted and brought to a focus at the retina.

The important agents in refraction in the eye are the surfaces of the cornea and the crystalline lens. Careful calculations have shown that the index of refraction of the aqueous humor is sensibly the same as that of the substance of the cornea, so that, practically, the refraction is the same as if the cornea and the aqueous humor were one and the same substance. The index of refraction of the vitreous humor is practically the same as that of the aqueous humor, both being about equal to the index of refraction of pure water. Re-

[1] VOLKMANN, *Sehen*, in WAGNER, *Handwörterbuch der Physiologie*, Braunschweig, 1846, Bd. iii., Erste Abtheilung, S. 334.

[2] See page 19.

fraction by the crystalline lens, however, is more complex in its mechanism; depending, first, upon the curvatures of its two surfaces, and, again, upon the differences in the consistence of different portions of its substance. In view of these facts, we may simplify the conditions of refraction in the eye by assuming the following arrangement:

The cornea presents a convex surface upon which the rays of light are received. At a certain distance behind its anterior border, is the crystalline, a double-convex lens, corrected, sufficiently for all practical purposes, both for spherical and chromatic aberration. This lens is practically suspended in a liquid with an index of refraction equal to that of pure water; as both the aqueous humor in front and the vitreous humor behind have the same refractive power. Behind the lens, in its axis and exactly in the plane at which the rays of light are brought to a focus by the action of the cornea and the lens, is the fovea centralis, which is the centre of distinct vision. The anatomical elements of the fovea are capable of receiving visual impressions, which are conveyed to the brain by the optic nerves. All impressions made upon other portions of the retina are comparatively indistinct; and the point of entrance of the optic nerve is insensible to light.[1] Inasmuch as the punctum cæcum is situated in either eye on the nasal side of the retina, in normal vision rays from the same object cannot fall upon both points at the same time. Thus, in binocular vision, the insensibility of the punctum cæcum does not interfere with sight; and the movements of the globe prevent any notable interference in vision, even with one eye. The sclerotic coat is for the protection of its contents

[1] Some writers state that the punctum cæcum possesses a faint sensibility to light, referring to the old experiments of Brewster made by throwing the image of a candle-flame upon the blind spot, and to recent observations with the ophthalmoscope, in support of this assertion. (LONGET, *Traité de physiologie*, Paris, 1869, tome ii., p. 904.) These observations, however, are fallacious, for the reason that it is impossible to exclude impressions made by the diffusion of light to the sensitive portions of the retina. The weight of experimental evidence is decidedly in favor of the absolute insensibility of the blind spot.

and for the insertion of muscles. The iris has an action similar to that of the diaphragm in optical instruments. The suspensory ligament of the lens, the ciliary body, and the ciliary muscle are for the fixation of the lens and its accommodation to distinct vision at different distances. The choroid is a dark membrane for the absorption of light, preventing confusion of vision from reflection within the eye.

Refraction by the cornea is effected simply by its external surface. The rays of light from a distant point are deviated by its convexity so that, if they were not again refracted by the crystalline lens, they would be brought to a focus at a point situated about $\frac{4}{10}$ of an inch behind the retina.[1] Without the crystalline lens, therefore, distinct vision is impossible, though the sensation of light is appreciated. In cases of extraction of the lens for cataract, the crystalline is supplied by a convex lens placed before the eye.

The rays of light, refracted by the anterior surface of the cornea, are received upon the anterior surface of the crystalline lens, by which they are still farther refracted. Passing through the substance of the lens, they undergo certain modifications in refraction dependent upon the differences in the various strata of the lens. These modifications have not been accurately calculated; but it is sufficient to state that they contribute to the accuracy of the formation of the retinal image and to the production of an image practically free from chromatic dispersion. As the rays pass out of the crystalline lens, they are again refracted by its posterior curvature, and are brought to a focus at the area of distinct vision.

The rays from all points of an object distinctly seen are brought to a focus, if the accommodation of the lens be correct, upon a restricted surface in the macula lutea; but the rays from different points cross each other before they reach the retina, and the image is consequently inverted. This is a fact capable of actual demonstration, as we have shown in treating of the formation of images in the eye.

[1] HELMHOLTZ, *Optique physiologique*, Paris, 1867, p. 89.

Calculating the curvatures of the refracting surfaces in the eye and the indices of refraction of its transparent media, it has been pretty clearly shown, by mathematical formulæ, that the eye, viewed simply as an optical instrument, and not practically, as the organ of vision, presents a certain degree of spherical and chromatic aberration;[1] but with these formulæ we have little to do in our purely physiological consideration of vision. As a matter of interest, however, we give a series of calculations, according to the best authorities upon the subject of physiological optics.[2]

In most calculations of the size of images, the positions of conjugate foci, etc., in normal and abnormal eyes, a schematic eye reduced by Donders,[3] after the example of Listing,[4] is regarded as sufficiently exact for all practical purposes. This simple scheme represents the eye as reduced to a single refracting surface, the cornea, and a single liquid assumed to have an index of refraction equal to that of pure water. The distance between what are called the two nodal points and between the two principal points of the dioptric system of the eye is so small, amounting to hardly $\frac{1}{100}$ of an inch, that it can be neglected. In this simple eye, we assume a radius of

[1] For an exceedingly interesting account of the eye considered as an optical instrument, see HELMHOLTZ, *L'œil considéré comme instrument d'optique.—Revue des cours scientifiques*, Paris, 1868–1869, tome vi., p. 211, *et seq.*

[2] HELMHOLTZ, *Optique physiologique*, Paris, 1867, p. 90, after LISTING.

Index of refraction of the atmosphere,	1
Index of refraction of the aqueous humor,	$\frac{103}{77}$
Index of refraction of the crystalline,	$\frac{16}{11}$
Index of refraction of the vitreous humor,	$\frac{103}{77}$
Radius of curvature of the cornea,	0·312 of an inch.
Radius of curvature of the anterior surface of the crystalline,	0·390 " "
Radius of curvature of the posterior surface of the crystalline,	0·234 " "
Distance between the anterior surface of the cornea and the anterior surface of the crystalline,	0·156 " "
Thickness of the crystalline,	0·156 " "

[3] DONDERS, *On the Anomalies of Accommodation and Refraction of the Eye*, The New Sydenham Society, London, 1864, p. 176.

[4] LISTING, *Dioptrik des Auges*, in WAGNER, *Handwörterbuch der Physiologie*, Braunschweig, 1853, Bd. iv., S. 493, *et seq.*

curvature of the cornea of about $\frac{1}{5}$ of an inch, and have a single optical centre situated $\frac{1}{5}$ of an inch back of the cornea, the "principal point" being in the cornea at the axis of vision. The posterior focal distance, that is, the focus at the bottom of the eye of rays that are parallel in the air, is about $\frac{4}{5}$ of an inch. The anterior focal distance, that is, of rays parallel in the vitreous humor, is about $\frac{3}{5}$ of an inch. The measurements in this simple eye can be easily remembered and used in calculations.

Astigmatism.

We have already alluded to an important peculiarity in the optical apparatus; viz., that the visual line does not coincide exactly with the axis of the eye.[1] There is still another normal deviation from mathematical exactness in the refraction of rays by the cornea and the crystalline lens, which is of considerable importance. If we place before the eyes two threads crossing each other at right angles in the same plane, one of these threads being vertical, and the other, horizontal, when the optical apparatus is adjusted so that one line is seen with perfect distinctness, the other is not well defined. In other words, when we accommodate for the vertical thread, the horizontal is indistinct, and *vice versa.* If the horizontal line be seen distinctly, in order to see the vertical, without modifying the accommodation, it must be removed to a greater distance. This depends chiefly upon a difference in the vertical and the horizontal curvatures of the cornea, so that the horizontal meridian has a focus slightly different from the focus of the vertical meridian. A condition opposite to that observed in the cornea usually exists in the crystalline lens; that is, the difference which exists between the curvatures of the lens in the vertical and the horizontal meridians is such that the deepest curvature in the lens is situated in the meridian of the shallowest curvature of the cornea. In this way, in normal eyes, the aberration of the lens has a

[1] See page 72.

tendency to correct the aberration in the cornea; but this correction is incomplete, and there still remains, in all degrees of tension of accommodation, a marked difference in the vision as regards vertical and horizontal lines.

The condition just described is known under the name of normal, regular astigmatism; but the aberration is not sufficiently great to interfere with distinct vision. The degree of regular astigmatism presents normal variations in different eyes. In some eyes there is no astigmatism; but this is rare. According to Donders, if the astigmatism amount to $\frac{1}{40}$ or more, it is to be considered abnormal;[1] which simply means that, beyond this point, the aberration interferes with distinct vision.

From the mere definition of regular astigmatism, it is evident that this condition and the degree to which it exists may easily be determined by noting the differences in the foci for vertical and horizontal lines, and it may be exactly corrected by the application of cylindrical glasses of proper curvature. Indeed, the curvature of a cylindrical glass, which will enable a person to distinguish vertical and horizontal lines with perfect distinctness at the same time, is an exact indication of the degree of aberration. Regular astigmatism, such as we have described, may be so exaggerated as to interfere very seriously with vision, when it becomes abnormal. This kind of aberration, however, which is dependent upon an abnormal condition of the cornea, is remediable by the use of properly-adjusted cylindrical glasses.

Irregular astigmatism, excluding cases of pathological deformation, opaque spots, etc., in the cornea, depends upon irregularity in the different sectors of the crystalline lens. Instead of a simple and regular aberration, consisting in a difference between the depth of the vertical and the horizontal curvatures of the cornea and lens, we have irregular variations in the curvatures of different sectors of the lens. As a

[1] DONDERS, *On the Anomalies of Accommodation and Refraction of the Eye*, The New Sydenham Society, London, 1864, p. 456.

consequence of this, when the irregularities are very great, there is impairment of the sharpness of vision. The circles of diffusion, which are regular in normal vision, become irregularly radiated, and single points appear multiple, an irregularity described by Donders, under the name of polyopia monocularis.[1] Accurate observations have shown that this condition exists to a very slight degree in normal eyes; but it is so slight as not to interfere with ordinary vision. In what is called normal, irregular astigmatism, the irregularity depends entirely upon the crystalline lens. If we place before the eye a card with a very small opening, and move this before the lens, so that the pencil of light falls successively upon different sectors, it can be shown that the focal distance is different for different portions. The radiating lines of light observed in looking at remote luminous points, as the fixed stars, are produced by this irregularity in the curvatures of the different sectors of the lens.

While regular astigmatism, both normal and abnormal, may be perfectly corrected by placing cylindrical glasses before the eyes, it is impossible, in the great majority of cases, to construct glasses which will remedy the irregular form.

For a complete account of the different forms of astigmatism, the reader is referred to the more elaborate works on ophthalmology. We have considered the subject briefly, as illustrating some of the aberrations in the normal eye, which, though they do not interfere materially with distinct vision, indicate clearly enough that the eye is by no means a perfect optical instrument.

[1] DONDERS, *On the Anomalies of Accommodation and Refraction of the Eye*, The New Sydenham Society, London, 1864, p. 543.

CHAPTER V.

MOVEMENTS OF THE IRIS—ACCOMMODATION.

Direct action of light upon the iris—Action of the nervous system on the iris—Mechanism of the movements of the iris—Accommodation of the eye to vision at different distances—Theories of accommodation—Changes in the crystalline lens in accommodation—Action of the ciliary muscle—Changes in the iris in accommodation.

THE movements of the iris are sufficiently simple, as well as the physiological conditions under which they take place; and it is only when we come to study the exact mechanism of the production of these movements through the nervous system, that the subject becomes complex, and, to a certain extent, obscure. As regards the movements themselves, the simple facts are as follows:

There are two physiological conditions under which the size of the pupil is modified: The first of these depends upon the amount of light to which the eye is exposed. When the quantity of light is small, the pupil is widely dilated, so as to admit as much as possible to the retina. When the eye is exposed to a bright light, the retina is protected by contraction of the iris. The muscular action by which the iris is contracted is characteristic of the smooth muscular fibres, as can be readily seen by exposing an eye, in which the pupil is dilated, to a bright light. Contraction does not take place instantly, but an appreciable interval elapses after the exposure, and a more or less gradual diminution in the size of the pupil is observed. This is seen both in solar and in artificial light. The second of these conditions depends, indirectly, upon the voluntary action of muscles. We have already seen,

in connection with the physiology of the third pair of nerves, that the effort of converging the axes of the eyes by looking at a very near object contracts the pupils.[1] We shall see, also, that the effort of accommodation of the eye for near objects produces the same effect, even when the eyes are not converged. This action will be fully considered under the head of accommodation.

One point relating to the anatomy of the iris is of great importance in connection with the physiology of its movements; and that is the question of the existence of dilator fibres. Upon this point there is some difference of opinion; but, as we stated in treating of the structure of the eye, the weight of anatomical authority is decidedly in favor of the existence of radiating fibres.[2] The physiology of the iris is much more easily understood, if we assume the existence of these fibres, and this is the view that we have adopted.

Direct Action of Light upon the Iris.—The variations in the size of the pupil under different physiological conditions are effected almost exclusively through the nervous system, either by reflex action from variations in the intensity of light, or by a direct influence, as in accommodation for distances; but it is nevertheless true that the muscular tissue of the iris will respond directly to the stimulus of light. In a memoir presented to the French Academy of Sciences, in 1847, it was shown by Dr. Brown-Séquard, that, in some of the lower animals, frogs, eels, etc., the iris continued to contract under the stimulus of light many days, even, after death. In frogs, the pupil was made to alternately contract and dilate, from fifty to one hundred times in a minute, in the eye extracted from the orbit.[3] Analogous phenomena have been observed by Harless in the human subject after death. These

[1] See vol. iv., Nervous System, p. 184.

[2] See page 53.

[3] BROWN-SÉQUARD, *Recherches expérimentales sur l'influence excitatrice de la lumière, du froid et de la chaleur sur l'iris.—Journal de la physiologie*, Paris, 1859, tome ii., p. 282.

observations are exceedingly interesting in connection with some of the contradictory experiments of physiologists upon the action of the motores oculorum upon the iris. Harless noted, in subjects dead of various diseases, from five to thirty hours after death, that the iris contracted under the stimulus of light; and he justly remarks that this is probably due to direct action upon its muscular tissue, and that it is not reflex, for the reason that the irritability of the nerves in warm-blooded animals disappears certainly in twenty hours after death. The experiments of Harless were made upon the two eyes, one being exposed to the light with the other closed. The contraction, however, took place very slowly, requiring an exposure of several hours.[1] This mode of contraction is very different from the action of the iris during life, but is precisely like the contraction observed by Bernard after division of the motor oculi communis, which is slow and gradual and undoubtedly depends upon the direct action of light upon the muscular fibres.[2]

Action of the Nervous System upon the Iris.—This subject, as far as it relates to the third pair, has been pretty fully considered in connection with the physiology of these nerves; and it is unnecessary to refer again in detail to the experiments which have already been cited. The reflex phenomena observed are sufficiently distinct. When light is admitted to the retina, the pupil contracts, and the same result follows mechanical irritation of the optic nerves. When the third pair of nerves has been divided, no such reflex phenomena are observed. It is well known, also, that division of the third nerves in the lower animals or their paralysis in the human subject produces permanent dilatation of the pupil, the iris responding, only in the slow and gradual manner already indicated, to the direct action of light.

The experiments made by direct stimulation of the third

[1] HARLESS, *Die Muskelirritabilität*, München, 1848.

[2] See vol. iv., Nervous System, p. 133.

nerve are somewhat contradictory. Some experimenters have noted that stimulation of these nerves produces immediate contraction of the pupil; but Bernard, Chauveau, and others failed to observe this as a constant phenomenon, and assume that, when contraction occurs, it is due to an extension of the irritation, either to the ophthalmic branch of the fifth or to the ciliary nerves passing to the iris from the ophthalmic ganglion.[1] The experiments upon the inferior animals were in the main confirmed in the human subject by Nuhn, in observations made upon the head of a decapitated criminal.[2]

Taking all the experimental facts into consideration, it is certain that the third nerve has an important influence upon the iris. Filaments from the ophthalmic ganglion animate the circular fibres, or sphincter, and these filaments derive their power from the third cranial nerve. If this nerve be divided, the iris becomes permanently dilated and is immovable, except that it responds very slowly to the direct action of light. The reflex action by which the pupil is contracted under the stimulus of light operates through the third nerve, and no such action can take place after this nerve has been divided. In view of these facts, there can be no doubt with regard to the nervous action upon the sphincter of the pupil, this muscle being animated exclusively by filaments from the motor oculi communis, coming through the ophthalmic ganglion.

We admit, with most modern anatomists, the existence of radiating muscular fibres in the iris, the action of which is antagonistic to the circular fibres, and which dilate the pupil. That these fibres are subjected to nervous influence is certain from experiments upon the sympathetic system.

The effects of division of the sympathetic in the neck have been treated of fully in connection with the general functions

[1] See vol. iv., Nervous System, p. 133.

[2] NUHN, *Versuche an einem Enthaupteten nebst erläuternden Versuchen an Thieren.—Zeitschrift für rationelle Medecin*, Heidelberg, 1853, Neue Folge, Bd. iii., S. 135.

of these nerves. It will be sufficient for our present purposes to state, in a general way, the influence of these nerves upon the movements of the iris. The original observations of division of the sympathetic in the neck, made by Pourfour du Petit, in 1712 and 1725, showed that this operation produced marked and permanent contraction of the pupil. These experiments have been repeatedly confirmed, and have been extended by more modern observers to show that, after division of the nerve, galvanization of the superior extremity produces enlargement of the pupil. They have also been repeated and confirmed by Nuhn[1] and by Wagner,[2] who operated upon the human subject a short time after decapitation.

There can be no doubt that the action of the sympathetic upon the pupil is directly antagonistic to that of the third pair, the former presiding over the radiating, or dilating muscular fibres; and the only question to determine is the course taken by the sympathetic filaments to the iris. Experiments on the influence of the fifth pair upon the pupil have been somewhat contradictory in different animals. In rabbits, section of this nerve in the cranial cavity produces contraction of the pupil; but in dogs and cats the same operation produces dilatation.[3] In the human subject, of course, it is impossible to determine this point by direct experiment; and the varying results obtained in observations upon different animals probably depend upon differences in the anatomical relations of the nerves.

The experiments of Donders, made upon rabbits, in which division of the fifth was found to produce contraction of the pupil, show that this influence is derived from connections of the sympathetic with the fifth at or near the ganglion of Gasser. In the first place, it had been shown by Bernard, that contraction of the iris follows division of the fifth, even

[1] NUHN, *Zeitschrift für rationelle Medecin*, Heidelberg, 1853, Neue Folge, Bd. iii., S. 135.

[2] WAGNER, *Note sur quelques expériences sur la partie cervicale du nerf grand sympathique, chez une femme décapitée.—Journal de la physiologie*, Paris, 1860, tome iii., p. 175.

[3] See vol. iv., Nervous System, p. 194.

if the third nerves have been extirpated;[1] which makes it evident that the influence of the fifth is direct, and not reflex through the third. Donders exposed and galvanized the sympathetic in the neck, to demonstrate the continued action of this nerve upon the iris. He then divided the fifth in the cranial cavity; and, after this division, in four out of eleven experiments, galvanization of the sympathetic in the neck failed to produce contraction of the pupil.[2] These experiments would seem to show that the filaments from the sympathetic which act upon the iris join the fifth, and that when the fifth is divided, the communication between this nerve and the radiating muscular fibres is cut off. It is somewhat difficult to explain the slight contraction of the pupil following galvanization of the sympathetic after division of the fifth in seven out of the eleven experiments, except by the fact, that, in many cases of division of the fifth in the cranial cavity, the sympathetic filaments are not included in the section.

There seem to be two distinct nerve-centres corresponding to the two sets of nerves which regulate the movements of the iris. One of these centres presides over the reflex contractions of the iris, and the other is the centre of origin of the nervous influence through which the pupil is dilated.

The mechanism of reflex contraction of the iris under the stimulus of light is sufficiently simple. An impression is made upon the retina, which is conveyed by the optic nerves to the centre of vision, and, in obedience to this impression, the sphincter of the iris contracts. If the optic nerves be divided, so that the impression cannot be conveyed to the centre, or if we divide the third pair, through which the motor stimulus is conveyed to the muscular fibres, no movements of the iris can take place. The centres which preside

[1] BERNARD, *Leçons sur la physiologie et la pathologie du système nerveux*, Paris, 1858, tome ii., pp. 208, 209.

[2] DONDERS, *Anomalies of Accommodation and Refraction of the Eye*, The New Sydenham Society, London, 1864, p. 582.

over these reflex phenomena are situated in the tubercula quadrigemina. In the remarkable experiments of Flourens upon the encephalic centres, it was shown that the iris loses its mobility after destruction of the tubercula.[1] This fact has been repeatedly confirmed by later experimenters. In birds, in which the decussation of the optic nerves is complete, this action is crossed, destruction of the tubercle upon one side producing immobility of the iris upon the opposite side; but in man, where the anatomical relations of the optic nerves upon the two sides are more complex, the crossed action is probably not so complete. In man, the axes of both eyes are habitually brought to bear upon objects, and it is well known that there is a physiological unity in the action of the two eyes in ordinary vision. We also observe that, when one eye only is exposed to light, the pupil becoming contracted under this stimulus, the pupil of the other eye also contracts. There is, indeed, a direct contraction and dilatation of the pupil of the eye which is exposed to the light, and an indirect, or "consensual" movement of the iris upon the opposite side. The consensual contraction occurs about $\frac{2}{5}$ of a second later than the direct action, and the consensual dilatation, about $\frac{1}{2}$ of a second later.[2]

Budge and Waller have shown that the filaments of the sympathetic which produce dilatation of the pupil take their origin from the spinal cord. In the spinal cord, between the sixth cervical and the second thoracic nerves, is situated the inferior cilio-spinal centre. When the spinal cord is stimulated in this situation, both pupils become dilated. If the cord be divided longitudinally and the two halves be separated from each other by a glass plate, stimulation of the right half produces dilatation of the right pupil, and *vice versa*.[3]

[1] FLOURENS, *Recherches expérimentales sur les propriétés et les fonctions du système nerveux*, Paris, 1842, p. 144, *et seq.*

[2] DONDERS, *Anomalies of Accommodation and Refraction of the Eye*, The New Sydenham Society, London, 1864, p. 573.

[3] Brown-Séquard assigns wider limits to the cilio-spinal centre. He states that "section of a lateral half of the spinal cord at the level of the fifth, the

This does not occur when the sympathetic in the neck has been divided. In addition to the inferior cilio-spinal centre, there is a superior centre, which is in communication with the superior cervical ganglion and is situated near the sublingual nerve. The influence of this centre over the pupil cannot be demonstrated by direct stimulation, because it is too near the origin of the fifth, irritation of which has an influence over the iris; but it is shown by division of its filaments of communication with the iris.[1]

Section and galvanization of the different nerves which regulate the movements of the iris have a certain influence upon its vascularity; and, indeed, it has been thought that contraction is in a measure due to congestion of its vessels, and dilatation, to an opposite condition. This view is adopted by some of those who deny the existence of the radiating muscular fibres. Assuming that the size of the pupil is, to a certain extent, affected by the condition of the vessels, it is evident that the extensive movements of the iris are due mainly to muscular action. It has been also shown by Brown-Séquard, that the changes in the iris produced by injection of its vessels are not to be compared with its physiological movements.[2] The changes in vascularity produced by dividing or galvanizing the sympathetic do not differ from the

sixth, and even sometimes as low down as the ninth or tenth dorsal vertebra, affects the iris like the section of the sympathetic, though in a less degree." (*Physiology and Pathology of the Central Nervous System*, Philadelphia, 1860, p. 144.)

[1] BUDGE, *Lehrbuch der speciellen Physiologie des Menschen*, Leipzig, 1862, S. 767, *et seq.*

According to the observations of Chauveau, the cilio-spinal centre acts on the iris as a reflex centre and not as a centre exerting a direct influence. He has shown that excitation of the sensitive roots coming from this region produces the same phenomena as irritation of the posterior columns of the cord, though with less intensity. (CHAUVEAU, *Action de la moelle épinère sur l'iris.—Journal de la physiologie*, Paris, 1861, tome iv., p. 383.)

[2] BROWN-SÉQUARD, *Recherches expérimentales sur l'influence excitatrice de la lumière, du froid et de la chaleur sur l'iris.—Journal de la physiologie*, Paris, 1859, tome ii., p. 452.

phenomena noted in experiments upon other portions of the sympathetic system.

Accommodation of the Eye to Vision at Different Distances.

The mechanism by which the eye is adjusted for distinct vision at different distances is one of the most interesting and important points connected with the physiology of the sight. At the present day, this point may be regarded as definitely settled, particularly since the variations in the thickness and the curvatures of the crystalline lens have been so accurately measured by Helmholtz. We shall have little to say with regard to the various theories of accommodation advanced by the older physiologists, except to indicate, in a very general way, the most plausible views that have been adopted from time to time by physiological writers. In the first place, we shall note certain physical laws and their application to the eye, which show the necessity for accommodation.

Supposing the eye to be adapted to vision at an infinite distance, in which the rays from an object, as they strike the cornea, are practically parallel, it is evident that the foci of the rays, as they form a distinct image upon the retina, are all situated at the proper plane. Under these conditions, in a perfectly normal eye, the image, appreciated by the individual or seen by means of the ophthalmoscope, is perfectly clear and distinct. If the foci be situated in front of the retina, the rays, instead of coming to a focus upon a point in the retina, will cross, and, from their diffusion, or dispersion, will produce indistinct vision. Under these circumstances, a distinct point is not perceived, but every point in the image is surrounded by an indistinct circle. These are called "circles of diffusion." If, now, the eye, adjusted for vision at an infinite distance, be brought to bear upon a near object, the rays from which are divergent as they strike the cornea, the image will be no longer distinct, but will be obscured by circles of diffusion. It is the adjustment by which these circles

of diffusion are removed that constitutes accommodation. This fact has been demonstrated by Helmholtz by means of the ophthalmoscope. "If the eye be adjusted to the observation of an object placed at a certain distance, it is found that the image of a flame, placed at the same distance, is produced with perfect distinctness upon the retina, and, at the same time, upon the illuminated plane of the image, the vessels and the other anatomical details of the retina are seen with equal distinctness. But, when the flame is brought considerably nearer, its image becomes confused, while the details of the structure of the retina remain perfectly distinct."[1]

It is evident that there is a certain condition of the eyes adapted to vision at an infinite distance, and that, for the clear perception of near objects, the transparent media must be so altered in their arrangement, or in the curvatures of their surfaces, that the refraction will be greater; for, without this, the rays would be brought to a focus beyond the retina. It is the mechanism of this adjustment to distances that has engaged the attention of physiologists for so many years.

To produce the necessary changes in the refractive power of the eye, physiologists have supposed a variety of conditions, none of their theories, however, presenting any positive basis in fact. It was thus with the theory that contraction of the pupil was sufficient for accommodation; that the curvature of the cornea was increased for near objects; that the lens was displaced, as in the adjustment of ordinary optical instruments; and the idea that the antero-posterior diameter of the eye was modified. The theory that has since been proven to be correct; namely, that of changes in the curvatures of the crystalline lens, was advanced by Thomas Young;[2] but the mechanism of these changes, supposed by Young to be due to the action of the lens itself, the constituent fibres of

[1] HELMHOLTZ, *Optique physiologique*, Paris, 1867, p. 123.

[2] YOUNG, *Observations on Vision, Read before the Royal Society*, London, May 30, 1793; and, *On the Mechanism of the Eye*, London, 1801.

which he supposed, with Leeuwenhoek, to be muscular, was not understood.

The changes in the eye, by which accommodation is effected, are now known to consist mainly in an increased convexity of the lens for near objects; and the only points in dispute are a few unimportant details in the mechanism of this action. The simple facts to be borne in mind in studying this question are the following:

When the eye is accommodated to vision at an infinite distance, the parts are passive.

In the adjustment of the eye for near objects, the convexities of the lens are increased by muscular action.

In accommodation for near objects, the pupil is contracted; but this action is merely accessory and is not essential.

The ordinary range of accommodation varies between a distance of about five inches and infinity.

Changes in the Crystalline Lens in Accommodation.—It is important to determine first the extent and nature of the changes of the lens in accommodation; and, by the ingenious experiments of the German physiologists, particularly those of Helmholtz, these changes have been accurately measured in the living subject. As the general result of these measurements, it was ascertained that the lens becomes increased in thickness in accommodation for near objects, chiefly by an increase in its anterior curvature, by which this surface of the lens is made to project toward the cornea. As the iris is in contact with the anterior surface of the lens, this membrane is made to project in the act of accommodation. The posterior curvature of the lens is also increased, but this is slight as compared with the increase of the curvature of its anterior surface. The distance between the posterior surface of the lens and the cornea is not sensibly altered. It is unnecessary to describe minutely the methods employed in making these calculations, and it is sufficient for our purposes to state that

it is done by accurately measuring the comparative size of images formed by reflection from the anterior surface of the lens. The results obtained by Helmholtz in observations upon three different persons are as follows:[1]

Eye.	Radius of Curvature of the Anterior Surface of the Lens.		Displacement of the Pupil in Accommodation for Near Objects.
	Distant Vision.	Near Vision.	
O. H.	0·4641 of an inch.	0·3354 of an inch.	0·0140 of an inch.
B. P.	0·3432 "	0·2701 "	0·0172 "
J. H.	0·4056 "		

The mechanism of the changes in the thickness and in the curvatures of the lens in accommodation can only be understood by keeping clearly in mind the physical properties of the lens itself and its anatomical relations. *In situ*, in what has been called the indolent state of the eye, the lens is adjusted to vision at an infinite distance, and is flattened by the tension of its suspensory ligament. After death, indeed, it is easy to produce changes in its form by applying traction to the zone of Zinn.[2] If we remember, now, the exact relations of the suspensory ligament, the ciliary muscle, and the lens, and keep in mind the tension within the globe, it is evident that when the ciliary muscle is in repose, the capsule will compress the lens, increasing its diameter and diminishing its convexity. It is in this condition that the eye is adapted to vision at an infinite distance. It is evident, also, that very slight changes in the convexity of the lens will be sufficient for the range of accommodation required. If we fix with the eye any near object, we are conscious of an effort, and the prolonged vision of near objects produces a sense of fatigue. This may be illustrated by the very familiar experiment of looking at a distant object through a gauze. When the object is seen distinctly, the gauze is scarcely perceived; but by an effort we can bring the eye to

[1] HELMHOLTZ, *Optique physiologique*, Paris, 1867, p. 157.
[2] HELMHOLTZ, *op. cit.*, p. 151.

ing perfect, and mentions another case, reported by Von Graefe, in which accommodation was not disturbed after loss of the entire iris.[1]

We have already noted the fact that the pupil contracts when the eyes are made to converge by the action of the muscles animated by the third pair of nerves;[2] and it is evident that convergence of the eyes always occurs in looking at very near objects. It becomes a question, then, whether the contraction of the pupil in accommodation for near objects be associated with the action of the third nerves, or with filaments from the ophthalmic ganglion, which supplies the nervous influence to the ciliary muscle. This seems to have been definitively settled by Donders, who demonstrated two important points: First, that increased convergence of the visual lines without change of accommodation makes the pupil contract, as is easily proven by simple experiments with prismatic glasses. Second, that when accommodation is effected without converging the visual axes, "each stronger tension is combined with contraction of the pupil."[3]

The action of the iris, as is evident from the facts just stated, is, to a certain extent, under the control of the will; but it cannot be disassociated, first, from the voluntary action of the muscles which converge the visual axes, and second, from the action of the ciliary muscle. Donders states that, by alternating the accommodation for a remote and a near object, he could voluntarily contract and dilate the pupil more than thirty times in the minute.[4] Brown-Séquard, in discussing the voluntary movements of the iris, mentions a case in which "the pupil could be contracted or dilated without changing the position of the eye or making an effort of adaptation for a long or a short distance.[5]

[1] Helmholtz, *op. cit.*, p. 151.

[2] See vol. iv., Nervous System, p. 134.

[3] Donders, *Anomalies of Accommodation and Refraction of the Eye.* The New Sydenham Society, London, 1864, p. 574.

[4] *Loc. cit.*

[5] Brown-Séquard, *Recherches expérimentales sur l'influence excitatrice de la lumière, du froid et de la chaleur sur l'iris.—Journal de la physiologie*, Paris, '59, tome ii., p. 287, note.

see the meshes of the gauze distinctly, when the impression of the distant object is either lost or becomes very indistinct.

Our knowledge of the action of the ciliary muscle is only to be arrived at theoretically and by studying the effects produced upon the lens. This muscle, it will be remembered, arises from the circular line of junction of the cornea and sclerotic, which is undoubtedly its fixed point, passes backward, and is lost in the tissue of the choroid, extending as far back as the anterior border of the retina. Most of the fibres pass directly backward, but some become circular or spiral. When this muscle contracts, the choroid is drawn forward, with, probably, a slightly spiral motion of the lens, the contents of the globe situated posterior to the lens are compressed, and the suspensory ligament is relaxed. The lens itself, the compressing and flattening action of the suspensory ligament being diminished, becomes thicker and more convex, by virtue of its own elasticity, in the same way that it becomes thicker after death, when the tension of the ligament is artificially diminished.

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[2] See vol. iv., Nervous System, p. 184.

[3] DONDERS, *Anomalies of Accommodation and Refraction of the Eye.* The New Sydenham Society, London, 1864, p. 574.

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As a farther evidence of the connection of accommodation with muscular action, cases are cited in works on ophthalmology in which there is paralysis of the ciliary muscle as well as cases in which the act of accommodation is painful.

An interesting phenomenon connected with accommodation is observed in looking at a near object through a very small orifice, like a pin-hole. The shortest distance at which we can see a small object distinctly is about five inches; but, if we look at the same object through a pin-hole in a card, it can be seen distinctly at the distance of about one inch, and appears considerably magnified. In this experiment, the card serves as a diaphragm with a very small opening, so that the centre of the lens only is used; and the apparent increase in the size of the object is probably due to the fact that its distance from the eye is many times less than the distance at which distinct vision is possible under ordinary conditions. It is well known that myopic persons, by being able to bring the eye nearer to objects than is possible in ordinary vision, can see minute details with extraordinary distinctness.

Accommodation in the Lensless Eye.—Within a few years, some very important and interesting pathological observations have been published in Germany upon accommodation without the lens; but one of the best-observed cases of this kind has been described by Dr. Edward G. Loring, Jr., of New York, who observed very accurately an instance of remarkable power of visual accommodation, in a person in whom both lenses had been removed for cataract. This case was reported to ophthalmological societies in 1869 and 1870. The observation is so interesting, and illustrates so beautifully the possible compensating action in the absence of the lens, that we give in full the following report, furnished by Dr. Loring, which has never before been published:

"In the spring of 1869, Miss E. W., eighteen years of age, consulted me for the purpose of procuring suitable

glasses. Five years before, when she was between twelve and thirteen years old, both eyes had been operated upon for cataract by the method of discission. After the absorption of the lenses had been completed, she was furnished with two pairs of glasses, one for the distance and the other for near work. Immediately after this, she went to California, and, shortly after going on board ship, she lost the glasses intended for near work, and had to rely entirely on her glasses for the distance. This pair had now become very much worn, and she simply wished to have them accurately measured, and a new pair made precisely like them. I found them to be convex, three and a half inch focus; and, with these glasses, vision was a little better than two-thirds of the normal standard.

"To my surprise, the patient then picked up a newspaper, and, pushing this back and forth, as persons ordinarily do who are trying glasses, remarked that she could see perfectly well, quite as well, in fact, as with the old pair. This drew my attention more particularly to the case, and the result of a more critical examination was as follows:

"With $+ \frac{1}{3\frac{1}{2}}$, the patient read with either eye fluently Snellen, XXX., and was able, with both eyes, to pick out most of the letters of XX. at twenty feet. She could read No. X. at ten feet, and No. V. at five feet.

"With the same glass, and with no change of position on the nose, she read No. I.½ Snellen fluently, holding the book naturally at twelve inches, which was about the distance at which she 'usually read.' The book was then gradually withdrawn, the patient reading aloud while this was done. It was found that twenty-one and a half inches was the greatest distance at which No. I.½ Snellen could be read. She read No. I. Jaeger at twenty inches. The book was then advanced inch by inch, the patient reading aloud, till the book was within five inches of the eye. Inside of this, reading became impossible. These experiments were tried over and over again by myself, and were finally repeated in the pres-

ence of a brother oculist. This would give the patient an adaptability of the eye for different distances from twenty feet (or parallel rays) to five inches; or, in other words, an accommodation of $\frac{1}{5}$ ($A = \frac{1}{5}$), and a relative accommodation for the very finest print from twenty inches to five ($A = \frac{1}{6\frac{2}{3}}$). My own range, measured at the same time, was from twenty to five inches (vision being, in my left eye, exceptionally large, $\frac{20}{12}$).

"A careful examination of the pupils showed that they were of the normal size, as were the movements of the iris in every respect. With the ophthalmoscope, the pupillary space was found in the right eye to be entirely free from any remains of capsule, while, in the left, a narrow rim of the whitened membrane just encroached on the upper pupillary margin, but not to such a degree as to limit the size of the pupil, and thus to act as a diaphragm. The media of the eye were perfectly clear, and the ophthalmoscopic appearances were normal in every respect.

"The patient promised to return, for the purpose of having the reflections of the cornea measured by the optometer, and the fact determined by the ophthalmoscope, whether, under accommodative efforts, the eyeball became elongated. This she failed to do, and the case, as stated above, was shortly after reported to the New York Ophthalmological Society, April 12, 1869, and, in July, 1870, to the American Ophthalmological Society. In the index of the transactions of the American Ophthalmological Society for that year, it appears as a case of 'Apparent Accommodation in a Lensless Eye.' The paper, however, does not appear in the text, having been withdrawn at the last moment, as there were hopes that another examination could be obtained, and the cause of the accommodation of the eye be definitely settled.

"Two years later, Prof. Förster published a series of similar cases[1] under the title of "Accommodative Power in

[1] FÖRSTER, *Accommodations-Vermögen bei Aphakie.—Klinische Monatsblätter für Augenheilkunde*, Erlangen, 1872, Bd. x., S. 39.

Aphakia." The present case, however, differs from those reported by Förster, in the fact that the range of accommodation was $\frac{1}{12\cdot8}$, larger than the maximum of any of his cases, and, from the very important fact that, whenever, in any of his cases, vision, both for the far and near, was taken, different glasses were used. In this case, the same glasses were used, worn in the same position, for all distances, from infinity up to five inches from the eye. So, too, in Woinow's[1] series of cases, the range of accommodation was taken only for the near, and amounted, on the average, to $\frac{1}{30}$.

"The only case which I know of that bears a close resemblance to the one above stated was reported by Arlt.[2] In this case, a young man, with convex $\frac{1}{8\frac{1}{2}}$, could read both at six and at twenty-four inches, and could recognize the hands of a steeple-clock, at a distance of more than five hundred paces, with the same glass; but, as neither the size of the print nor that of the clock is given, no accurate conclusions can be drawn from the case.

"The case observed by me would then appear to be the first—as it is certainly the most remarkable—subjected to the recognized standard test of vision. Here the amount of accommodation was equal to that of a normal eye in a young person; and it would seem impossible that the ability to read the finest print at five inches, even taking into consideration the magnifying power of the glass, could be due to the overcoming of the circles of dispersion, as is claimed by the great majority of physiologists.

"Förster's views and the correctness of his tests have been objected to latterly by the following writers, cited by Woinow; viz., Donders, Mannhardt, Coert, and Abadie.[3]

"Woinow, on the other hand, while he thinks that, in the normal eye, accommodation is performed solely by the lens,

[1] Woinow, *Das Accommodations-Vermögen bei Aphakie.—Archiv für Ophthalmologie*, Berlin, 1873, Bd. xix., S. 107, *et seq.*

[2] Arlt, *Die Krankheiten des Auges*, Prag, 1858, Bd. ii., S. 348.

[3] Woinow, *op. cit.—Archiv für Augenheilkunde*, Berlin, 1873, Bd. xix., S. 108.

believes that some aphakial eyes acquire accommodative power, which is necessarily brought about through the agency of four factors; namely, the cornea, the vitreous, the action of the ciliary muscle and its effect on the bottom of the eye, and, finally, the effect of the external muscles of the globe. Woinow eliminates, from this group, the cornea, while Förster makes it the chief, if not the sole agent. In two cases, Woinow was able to observe the reflections from the anterior surface of the vitreous humor, which, in the absence of the lens, was convex, as was shown by the image being upright. These reflections were too weak to be measured by the optometer; but they were seen to become smaller when efforts were made to see at close distances.

"It is to be regretted, and it certainly appears a little strange, that, in neither Förster's nor Woinow's cases, was either the optometer or ophthalmoscope used in the elucidation of this problem. But, while Woinow's cases are, as he himself says, not conclusive, yet they seem, like Arlt's, Förster's, and the one just related, to substantiate the view that occasionally a considerable, if not a large degree of accommodation may exist, even in a lensless eye."

CHAPTER VI.

BINOCULAR VISION, ETC.

Erect impressions produced by images inverted upon the retina—Single vision with both eyes—Corresponding points—The horopter—Appreciation of distance and the form of objects—Mechanism of the stereoscope—Binocular fusion of colors—Duration of luminous impressions—Irradiation—Movements of the eyeball—Muscles of the eyeball—Axes of rotation of the globe for the different sets of muscles—Action of the recti muscles—Action of the oblique muscles—Associated action of the different muscles of the eyeball—Parts for the protection of the eyeball—Eyelids—Muscles which open and close the eyelids—Conjunctival mucous membrane—Lachrymal apparatus—Composition of the tears.

In beginning our study of the optical apparatus, it was stated that we did not propose to treat of the subject exhaustively, and that we should omit the consideration of certain points, interesting in themselves, but not essential to a comprehension of the physiology of vision. We have thus far considered pretty fully the anatomy of the eye, a clear idea of which is a necessary preparation for the study of its physiology. We have also studied the action of the eye as an optical instrument, with the mechanism of refraction, the formation of images on the retina, the movements of the iris, and the mechanism of accommodation. In this chapter, we shall treat of binocular vision, the duration of luminous impressions, irradiation, the movements of the eyeball, and the parts for the protection of the eye. It does not seem desirable to consider even these points with great elaborateness. If we have become thoroughly acquainted with the mechanism of the formation of images upon the retina and the physiological action of the different parts of the optical

apparatus, it will be sufficient to note the action of both eyes, as contrasted with the action of one, in normal vision, without discussing fully the multitude of curious observations made with the stereoscope; and we can readily comprehend the action of muscles by which the axis of vision is directed toward different objects, without entering into a discussion of abstruse mathematical calculations with regard to the exact centre of rotation, the law of torsions, and other points connected with physiological optics. These are questions, however, of great interest to ophthalmologists, and are fully discussed in elaborate special treatises.

We shall allude briefly, in this connection, to a question which has long engaged the attention of physiologists, and one which, we cannot but think, has been made the subject of much unprofitable speculation. It is a matter of positive demonstration that the images of objects seen are inverted as they appear upon the retina. Why is it, however, that objects are appreciated as erect, when their images are thus inverted? With a knowledge of the fact that the appreciation of impressions made upon the nerves of special sense is capable of education and is corrected by experience, it seems hardly necessary to enter into an elaborate discussion of this point. We appreciate with accuracy the density of objects, the direction of sounds, differences in musical tones, the taste of sapid substances, odors, etc., as the result, to a great degree, of education. In the same way, probably, we acquire the power of noting the position of objects in vision; but even this supposition is not necessary to explain the phenomenon of direct vision by means of inverted images. The following paragraph, quoted from Giraud-Teulon, is a simple expression of facts, and shows the absurdity of the elaborate theoretical explanations made by many of the earlier writers:

"If the objects seen mark their image upon the retina, each one in a proper secondary axis; if, on the other hand, the retina appreciates these, *independently of ourselves*, in

these same secondary axes, which all cross at the same point, it is evident that an exact or *erect* sensation, as well as the object which produces it, should necessarily correspond to an inverted or reversed image. But it is neither habit, education, nor information derived from the sense of touch, that enables us, as it is said, to see objects *erect* by means of *reversed images*. The retina sees or localizes objects where they are; that is what we call 'erect.' If the picture be reversed, it is a mere matter of geometry."[1]

In discussing the same question, Helmholtz says that "our natural consciousness is completely ignorant even of the existence of the retina and of the formation of images: how should it know any thing of the position of images formed upon it?"[2]

Binocular Vision.

We have thus far considered the mechanism of the eye and its action as an optical instrument, in simple, or monocular vision. It is evident, however, that we habitually use both eyes, and that their axes are practically parallel in looking at distant objects and are converged when objects are approached to the nearest point at which we have distinct vision. In fact, an image is formed simultaneously upon the retina of each eye, but is nevertheless appreciated as a unit. If the axis of one eye be slightly deviated by pressure upon the globe, so that the images are not formed upon corresponding points upon the retina of each eye, our vision is more or less indistinct, and is double. In strabismus, when this condition is recent, temporary, or periodical, as in recent cases of paralysis of the external rectus muscle, when both eyes are normal, there is double vision. When the strabismus is permanent and has existed for a long time, double vision may not be observed, unless the subject direct the attention strongly to this point. As it is usual, in such cases, for one

[1] GIRAUD-TEULON, *La vision binoculaire.—Revue des cours scientifiques*, Paris, 1867–1868, tome v., p. 223.

[2] HELMHOLTZ, *Optique physiologique*, Paris, 1867, p. 771.

eye to be much superior to the other in acuteness of vision, an object is fixed with the better eye, and its image is formed upon the fovea. The image formed upon the retina of the other eye is indistinct, and in many instances is habitually disregarded; so that, practically, the subject uses but one eye, and presents the errors of appreciation which attend monocular vision, such as a want of accurate estimation of the solidity and distance of objects.[1] It is stated, as the rule, that when strabismus of long standing is remedied, as far as the axes of the eyes are concerned, by an operation, binocular vision is not restored; but the experiments necessary to the accurate determination of this point are exceedingly delicate and must be made with great care.[2] This is explained upon the supposition that the functional power of the retina of the affected eye has been gradually and irrecoverably lost from disuse. In normal binocular vision, the images are formed upon the fovea centralis of each eye; that is, upon corresponding points, which are, for each eye, the centres of distinct vision.

It is hardly necessary to speculate with regard to the reason why two images, one upon each retina, convey the impression of a single object. We appreciate a sound with both ears; the impression of a single object is received by the sensory nerves of two or more fingers; the olfactory nerves upon the two sides are simultaneously concerned in olfaction; and, in the same way, when we look at a single object with both eyes, the brain appreciates a single image. We shall see, however, that the concurrence of both eyes is necessary to the exact appreciation of distance and form; and, when the two images are formed upon corresponding

[1] Prof. H. D. Noyes has stated to me verbally, that, in some cases of strabismus of long standing, there has seemed to exist binocular vision, which is to be explained only upon the supposition that a new fovea centralis, as it were, has been formed in one eye, by increasing the sensibility of the retina at a new point through constant use.

[2] STELLWAG VON CARION, *Treatise on the Diseases of the Eye*, New York, 1868, pp. 705, 713.

points, the brain receives a correct impression of a single object. When our vision is perfectly normal, the sensation of the situation of any single object is referred to one and the same point, and we cannot receive the impression of a double image, unless the conditions of vision be abnormal.

Corresponding Points.—While it requires no argument, after the statements we have just made, to show that an image must be formed upon the fovea of each eye in order to produce the effect of a single object, it becomes important to ascertain how far it is necessary that the correspondence of points be carried out in the retina. This leads to considerations of very great interest and importance. It is almost certain that, for absolutely perfect, single vision with the two eyes, the impressions must be made upon exactly corresponding points, even to the ultimate sensitive elements of the retina. We may suppose, indeed, that each rod and each cone of one eye has its corresponding rod and cone in the other, situated at exactly the same distance in corresponding directions from the visual axis.[1] When the two images of an object are formed upon these corresponding points, they appear as one; but, when the images do not correspond, the impression is as though the images were formed upon different points in one retina, and, of necessity, they appear double.

The effect of a slight deviation from the corresponding points may be illustrated by the following experiment: We fix a small object, like a lead-pencil, held at a distance of a few inches, with the eyes, and see it distinctly as a single object; we hold in the same line, a few inches farther removed, another small object; when the first is seen distinctly, the second appears double; we fix the second with

[1] It is interesting to note, in this connection, the point, shown by cases of hemiopsia, that the fibres from the optic tract upon one side are probably connected with the outer vertical half of the retina of the same side, and with the inner vertical half of the retina of the opposite side. This shows that the outer half of one retina corresponds to the inner half of the other. (See page 41.)

the eyes, and the first appears double. It is evident here, that when the axes of the eyes bear upon one of these objects, the images of the other must be formed a certain distance from the corresponding retinal points.

The Horopter.—The above-mentioned experiment enables us to understand the situation of the horopter. If we fix both eyes upon any object directly in front and keep them in this position, a similar object moved to one side or the other, within a certain area, may be seen without any change in the direction of the axis of vision; but the distance from the eye at which we have single vision of this second object is fixed, and, at any other distance, the object appears double. The explanation of this is, that, at a certain distance from the eye, the images are formed upon corresponding points in the retina; but, at a shorter or longer distance, this cannot occur. This illustrates the fact that there are corresponding points throughout the sensitive layer of the retina, as well as in the fovea centralis. By these experiments, the following facts have been ascertained: With both eyes fixed upon an object, another object moved to one side or the other can be distinctly seen only when it is carried in a certain curved line. On either side of this line, the object appears double. This line, or area, for the line may have any direction, is called the horopter. It was supposed at one time to be a regular curve, a portion of a circle drawn through the fixed point and the points of intersection of the rays of light in each eye. Though it has been ascertained that the line varies somewhat from a regular curve, and also varies in different meridians, this is due to differences in refraction, etc., and the principle is not altered.

It is undoubtedly true that education and habit have a great deal to do with the correction of visual impressions and the just appreciation of the size, form, and distance of objects. If we may credit the account of the remarkable

case of Caspar Hauser, who is said to have been kept in total darkness and seclusion, from the age of five months until he was nearly seventeen years old, the appreciation of size, form, and distance is acquired by correcting and supplementing the sense of sight by experience, even in binocular vision. This boy at first had no idea of the form of objects, nor of distance, until he had learned by touch, by walking, etc., that certain objects were round, others square, and had actually traversed the distance from one object to another. At first, all objects appeared to be, as it were, painted upon a screen.[1] Such points as these it would be impossible for us to accurately observe in infants; but we have all seen young children grasp at remote objects, apparently under the impression that they were within reach. It must be admitted, however, that the case of Caspar Hauser is rather indefinite; but it is certain that, even in the adult, education and habit enable us to greatly improve the faculty of estimating distances.

The important questions for us now to determine relate to the differences between monocular and binocular vision in the adult. We may see an object distinctly with one eye; but are we able, from an image made upon one retina, to appreciate all its dimensions and its exact locality?

Accurate observations bearing upon this question leave no doubt of the fact that monocular vision is incomplete and inaccurate, and that it is only when two images are formed, one

[1] *Caspar Hauser. An Account of an Individual kept in a Dungeon, separated from all Communication with the World, from early Childhood to about the Age of Seventeen. Drawn up from Legal Documents.* By Anselm von Feuerbach, President of one of the Bavarian Courts of Appeal, etc. Translated from the German. Second Edition, Boston, 1833.

As far as we can judge, the history of this remarkable case seems to be authentic, though the scientific observations are obscure and indefinite. The account of the gradual development of correct vision is on page 88.

Helmholtz cites several cases of recovery of sight at a relatively advanced age in persons born blind, which show that the ideas of distance, form, etc., are gradually acquired by experience. (Helmholtz, *Optique physiologique*, Paris, 1867, p. 749.)

upon each retina, that vision is perfect. We cannot better illustrate the truth of this proposition and the exact condition of our positive knowledge upon this important point, than by quoting in full the facts and arguments advanced by Giraud-Teulon:[1]

"Monocular vision only indicates to us immediately *visual direction*, and not precise locality. At whatever distance a luminous point may be situated in the line of direction, it forms its image upon the same point in the retina.

"In the physiological action of a single eye, in order to arrive at an idea of the distance of a point in a definite direction, we have only the following elements:

"1. The consciousness of an effort of accommodation.

"2. Our own movement in its relations to the point observed.

"3. Facts brought to bear from recollection, education, our acquired knowledge with regard to the form and size of objects: in a word, experience.

"4. The geometric perspective of form and position.

"5. Aërial perspective.

"All these are elements wanting in precision and leaving the problem without a decisive solution.

"And, indeed:

"We place before one of our eyes, the other being closed, the excavated mould of a medallion: we do not hesitate, after a few seconds, to mistake it for the relief of the medallion. This illusion ceases at the instant that both eyes are opened.

"Or again:

"A miniature, a photograph, a picture, produces for a single eye a perfect illusion; but, if both eyes be open, the picture becomes flat, the prominences and the depressions are effaced.

"We may repeat the following experiment described by

[1] Giraud-Teulon, *La vision binoculaire.—Revue des cours scientifiques*, Paris, 1867–1868, tome v., p. 225, *et seq.*

Malebranche: 'Suspend by a thread a ring, the opening of which is not directed toward us; step back two or three paces; take in the hand a stick curved at the end; then, closing one eye with the hand, endeavor to insert the curved end of the stick within the ring, and we shall be surprised at being unable to do in a hundred trials what we should believe to be very easy. If, indeed, we abandon the stick and endeavor to pass one of the fingers through the ring, we shall experience a certain amount of difficulty, although it is very near. This difficulty ceases at the instant that both eyes are opened.' (MALEBRANCHE, *Des sens*, liv. 1er, chap. ix.)

"As regards precision, exactitude of information concerning the relative distance of objects, that is to say, the idea of the *third dimension* or of *depth*, there is then a notable difference between binocular vision and that which is obtained by means of one eye alone.

"This difference is brought strikingly into view by the following remarks of Malebranche, remarks which themselves imply an anticipated idea of the very principles of associated vision.

"Returning to the experiment with the ring, Malebranche adds the following judicious remarks: 'But we must certainly note that I have said that we endeavor to pass through the ring from the side, and not by a straight line from the eye to the ring; for then there would be no difficulty, and indeed it would be still easier to accomplish this with one eye closed than with both eyes opened, because that guides us.' (Principle of direction, without localization.) 'Therefore, one could say that the difficulty experienced in passing through a ring from the side, with but one eye opened, is because, the other eye being closed, the angle of which I have spoken (the angle of convergence of the optical axes) is not known; for it is not enough, in order to recognize the size of an angle (read *in order to recognize a triangle*), to know the size of the base and of the angle formed by one of the sides with the base, which is known in the pre-

ceding experiment; but it is necessary in addition to know the angle formed by the other side with the base, or the length of one of the sides, which cannot be known *exactly* except by opening the other eye. The arrangement of the two eyes as regards the angle formed by the visual rays (read *the lines of vision*) which meet each other at the object is then one of the best and most universal means made use of by the intelligence to judge of *the distance of things*.'"

From the above extract, which is entirely in accordance with our present knowledge, it is evident that an accurate idea of the distance of objects cannot be obtained except by the use of both eyes, and this fact will explain, in part, the errors of monocular vision, when we look with one eye upon objects in relief; for, under these conditions, we cannot determine with accuracy whether the points in relief be nearer or farther from the eye than the plane surface. This will not fully explain, however, the idea of solidity of objects which we obtain by the use of both eyes; for the estimation of distance is obtained by bringing the axes of both eyes to bear upon a single object, be it near or remote. The fact is, as was distinctly stated by Galen, in the second century,[1] that, when we look at any solid object not so far removed as to render the visual axes practically parallel, we see with the right eye a portion of the surface which is not seen with the left eye, and *vice versa*. The two impressions, therefore, are not identical for each retina; the image upon the left retina including a portion of the left side of the object not seen by the right eye, the right image in the same way including a portion of the right surface not seen by the left eye. These slightly dissimilar impressions are fused, as it were, produce the impression of a single image, when vision is perfectly normal, and this gives the idea of relief or solidity, enabling us to appreciate exactly the form of objects, when they are not too remote.

[1] GALIEN, *Œuvres anatomiques, physiologiques et médicales, par* DAREMBERG, Paris, 1854, tome i., p. 640, *et seq*.

The fact just stated is of course a mathematical necessity in binocular vision for near objects; but the actual demonstration of the fusion of two dissimilar images and the consequent formation of a single image giving the impression of solidity was made by the invention of the stereoscope, by Wheatstone.[1] The principle of this instrument is very simple. Two pictures are made, representing a solid object, one viewed slightly from the right side, and the other, slightly from the left, so as to imitate the differences in the images formed upon the two retinæ. These pictures are so placed in a box that the image of one is formed upon the right retina, and the other, upon the left. When these conditions are accurately fulfilled, we see but a single image, and this conveys to the mind the perfect illusion of a solid object. Experiments with the stereoscope are so familiar that they need hardly be dwelt upon. With most persons, an apparatus is necessary to shut off disturbing visual impressions; but some individuals are able to fuse two images in this way, placed in proper position, without the aid of an instrument, by a simple effort of the will.

The invention of the stereoscope has led to many curious and interesting experiments, especially since the art of photography has enabled us to produce pictures in any position with absolute accuracy; but a simple statement of the principle upon which the instrument is constructed illustrates the mechanism of binocular vision in the appreciation of the form of objects. Experience, the aid of the sense of touch, etc., enable persons with but one eye to get a notion of form, but the impressions are never entirely accurate in this regard, although, from habit, this defect occasions little or no inconvenience. A striking illustration of these points is afforded by the binocular microscope, which, especially with low magnifying powers, produces a startling impression of relief.

As we have just remarked, the stereoscope affords a satis-

[1] WHEATSTONE, *Contributions to the Physiology of Vision.—Philosophical Transactions*, London, 1838, vol. xxxviii., p. 371, *et seq.*

factory explanation of the mechanism of the eye in the appreciation of the form of objects; but, notwithstanding this, a theory has been proposed, and is adopted by some writers, that we obtain an idea of form by rapidly and insensibly directing the eyes successively toward different points on the surface of objects. It is difficult to understand how the eye can make these rapid movements, but the question is definitively settled by a very simple fact demonstrated by Dove, Helmholtz, and others. In an article on visual perception, by Helmholtz, it is stated that stereoscopic effect is recognized when two pictures are seen illuminated by an electric spark, the duration of which does not amount to the four-thousandth part of a second, so short, indeed, that a falling body appears absolutely motionless.[1] Under these conditions, displacement of the line of vision would seem to be impossible.

We shall conclude our discussion of binocular vision and the stereoscope with a brief account of some experiments upon the binocular fusion of colors, which are very curious, though they have no very important bearing upon the physiology of the eye in ordinary vision. Though an opposite opinion is held by some experimenters, Helmholtz, with many others, states that when one color is seen with one eye and another color with the other eye, in the stereoscope, the impression is not of a single color resulting from the combination of the two.[2] It is true that there is an imperfect mingling of the two colors, but this is very different from the resulting color produced by the actual fusion of the two. There is, in other words, a sort of confusion of colors, without the complete combination with which we are familiar in ordinary experiments. One additional point of interest, however, is that the binocular fusion of two pictures, unequally illuminated or of different colors, produces a single

[1] HELMHOLTZ, *Les perceptions visuelles.—Revue des cours scientifiques*, Paris, 1868–1869, tome vi., p. 422; and, *Optique physiologique*, Paris, 1867, p. 937.

[2] HELMHOLTZ, *Optique physiologique*, Paris, 1867, p. 976.

image of a peculiar lustre, even when both surfaces are dull. This may be very elegantly shown by making a stereoscopic combination of images of crystals, one with black lines on a white ground, and the other with white lines on a black ground. The resulting image has then the appearance of dark, brilliant crystals, like graphite.[1]

Duration of Luminous Impressions.

The time necessary for vision is exceedingly short; so short, indeed, that it almost passes our powers of comprehension. Taking advantage of the very delicate methods of chronometric observations now employed by physicists, it has been shown by Prof. Rood that the letters on a printed page are distinctly seen when illuminated by an electric spark, the duration of which was measured and found to be not more than forty billionths of a second.[2] By reference to page 74, it will be seen that the waves of light strike the eye at the rate of over five hundred millions of millions in a second; so that, even in the period indicated by Prof. Rood, an immense number of waves have time to impinge upon the retina.

We have long been familiar with the fact that an impression made upon the retina endures for a period of time that can readily be measured, and that its duration bears a certain degree of relation to the intensity of the luminous excitation. If, after looking fixedly at a very bright object, we suddenly produce complete obscurity, the object is more or less distinctly seen, when the rays have ceased to pass to the eye, and the image fades away gradually. When we produce a rapid succession of images, they may be, as it were, fused into one, as the spokes of a rapidly-revolving wheel are indistinct and produce a single impression. This is due to the persistence of the successive retinal impressions; for, if a revolving wheel, or even a falling body, be illuminated for the

[1] HELMHOLTZ, *Optique physiologique*, Paris, 1867, p. 983.

[2] ROOD, *On the Amount of Time necessary for Vision.—American Journal of Science and Arts*, New Haven, 1871, Third Series, vol. ii., p. 159.

brief duration of an electric spark, it appears absolutely stationary, as the period of time necessary for perfectly distinct vision and the duration of the illumination are so short, that there is no time for any appreciable movement of the object. The familiar experiments made with revolving disks beautifully illustrate these points. In a disk marked with alternate radiating lines of black and white, the rays become entirely indistinguishable during rapid revolution, and the disk appears of a uniform color, such as would be produced by a combination of the black and white. Very beautiful effects of artificial combination of colors may be produced in this way, the resultant color appearing precisely as if the individual colors had been ground together. It is also interesting, in this connection, to note that the duration of the retinal impressions varies considerably for the different colors. This fact was observed some years ago by Plateau,[1] and was confirmed by Emsmann,[2] there being some slight variations in the comparative results obtained by these two experimenters. According to Emsmann, the duration for yellow is 0·25 of a second; for white, 0·25 of a second; for red, 0·22 of a second; and for blue, 0·21 of a second.

It is unnecessary to describe farther in detail the well-known phenomena which illustrate the point under consideration. The circle of light produced by rapidly revolving a burning coal, the track of a meteor, and other illustrations are sufficiently familiar, as well as many scientific toys producing optical illusions of various kinds.

Irradiation.—It has been observed that luminous impressions are not always confined to the elements of the retina directly involved, but are sometimes propagated to those immediately adjacent. This gives to objects a certain degree of

[1] Plateau, *Ueber einige Eigenschaften der vom Lichte auf das Gesichtsorgan hervorgebrachten Eindrücke.—Annalen der Physik und Chemie*, Leipzig, 1830, Bd. xx., S. 309.

[2] Emsmann, *Ueber die Dauer des Lichteindrucks.—Annalen der Physik und Chemie*, Leipzig, 1854, Bd. xci. (vierte Reihe, Bd. i.), S. 616.

amplification, which is generally in proportion to their brightness. An illustration of this is afforded by the simple experiment of looking at two circles, one black on a white ground, and the other white on a black ground. Although the actual dimensions of the two circles are identical, the irradiation of rays from the white circle makes this appear the larger. In a circle with one half black and the other white, the white portion will appear larger for the same reason. This deception increases sensibly when we look steadily at the object. These phenomena are due to what has been called by physiologists irradiation; and their explanation is very simple. It is probable that luminous impressions are never confined absolutely to those parts of the retina upon which the rays of light directly impinge, but that the sensitive elements immediately contiguous are always more or less involved. In looking at powerfully illuminated objects, the irradiation is considerable, as compared with objects which send fewer luminous rays to the eye.

In experiments analogous to those just described, made with strongly colored objects, it has been observed that the border of irradiation takes a color complementary to that of the object itself. This is particularly well marked when the objects are steadily looked at for some time. Illustrations of this point also are very simple. If we looked fixedly at a red spot or figure on a white ground, we soon see surrounding the red object a faint areola of a pale green; or, if the image be yellow, the areola will appear pale blue. These appearances have been called accidental areolæ.

Movements of the Eyeball.

The eyeball nearly fills the cavity of the orbit, resting, by its posterior portion, upon a bed of adipose tissue, which is never absent, even in extreme emaciation. Outside of the sclerotic, is a fibrous membrane, the tunica vaginalis oculi, or capsule of Tenon, which is useful in maintaining the equilibrium of the globe. This fibrous membrane surrounds the

posterior two-thirds of the globe, and is loosely attached to the sclerotic. It is perforated by the optic nerve posteriorly, and by the tendons of the recti and oblique muscles of the eyeball in front, being reflected over these muscles. It is also continuous with the palpebral ligaments and is attached by two tendinous bands to the border of the orbit at the internal and the external angles of the lids.

The muscles which move the globe are six in number for each eye. These are, the external and internal recti, the superior and inferior recti, and the two oblique muscles. The four recti muscles and the superior oblique arise posteriorly from the apex of the orbit. The recti pass directly forward by the sides of the globe and are inserted by short, tendinous bands into the sclerotic, at a distance of from one-fourth to one-third of an inch from the margin of the cornea. The superior oblique, or trochlearis muscle passes along the upper and inner wall of the orbit to a point near the inner angle. It here presents a rounded tendon, which passes through a ring, or pulley of fibro-cartilage; and it is from this point that its action is exerted upon the globe. From the pulley, or trochlea, the tendon becomes flattened, passes outward and backward beneath the superior rectus, and is inserted into the sclerotic, about midway between the superior and the external rectus and just behind the equator of the globe. The inferior oblique muscle arises just within the anterior margin of the orbit, near the inner angle of the eye, and passes around the anterior portion of the globe, beneath the inferior rectus and between the external rectus and the eyeball, taking a direction outward and slightly backward. Its tendon is inserted into the sclerotic, a little below the insertion of the superior oblique. The general arrangement of these muscles is shown in Fig. 8.

The various movements of the eyeball are easily understood by a study of the associated movements of the muscles just enumerated, at least, as far as is necessary to the comprehension of the mechanism by which the eyes are directed

toward any particular object. We have already seen that the centre of exact vision is in the fovea; and it is evident that, in order to see any object distinctly, it is necessary to bring it within the axes of vision of both eyes. As the

FIG. 8.

Muscles of the eyeball.—1, attachment of the tendon connected with the inferior rectus, internal rectus, and external rectus; 2, external rectus divided and turned downward to expose the inferior rectus; 3, internal rectus; 4, inferior rectus; 5, superior rectus; 6, superior oblique; 7, pulley and reflected portion of the superior oblique; 8, inferior oblique; 9, levator palpebri superioris; 10, 10, middle portion of the levator palpebri superioris; 11, optic nerve. (SAPPEY, *Traité d'anatomie*, Paris, 1868, tome ii., p. 113.)

globe is so balanced in the orbit as to be capable of rotation, within certain limits, in every direction, we have only to note the exact mode of action of each of the muscles, in order to comprehend how the different movements are accomplished.

It is sufficient for our purposes to admit that, approximatively, there is a common axis of rotation for each pair of muscles; but the movements of the globe have been studied much more minutely than this, with reference particularly to the effects of paralysis of different muscles. The points thus

developed are interesting and important in their pathological bearing, but the intricate mathematical calculations involved are not essential to our comprehension of the simple acts by which the axis of vision is moved in various directions. It is not necessary to discuss the exact location of the centre of rotation of the eye, the mathematical formulæ illustrating what are known as the laws of rotation, or the law of torsions, especially as some of these points are still unsettled, notwithstanding the elaborate and delicate observations of Donders, Helmholtz, and many others. In the admirable work of Helmholtz, to which we have so often referred, we find the following statement, which will form the basis of our study of the ocular movements:

"By the diversified combination of the action of the six muscles, not only may the axis of the eye be turned in all directions, but the eye may, in addition, receive movements of rotation around this axis. If we have assumed for each pair of muscles a common axis of rotation, it is that this supposition seems admissible, at least as a first approximation, and that it simplifies to a remarkable degree the examination of the movements which the muscles of the eye have to perform."[1]

Under ordinary conditions, in the human subject, the action of the six ocular muscles is confined to the movements of rotation and torsion of the globe. It is said that, in the human subject, there is no such thing as protrusion of the eye, from general relaxation of these muscles, and that it is impossible, by a combined action of the four recti muscles, to retract the globe in the orbit;[2] but those who have operated upon the eyes assert positively that this statement is erroneous; and that the globe is almost always suddenly and powerfully drawn within the orbit when a painful impression is made upon the cornea. This is stated as a matter of common observation by ophthalmic surgeons.[3]

[1] HELMHOLTZ, *Optique physiologique*, Paris, 1867, p. 41.

[2] HELMHOLTZ, *op. cit.*, p. 596. [3] Oral communication from Prof. Noyes.

The extent to which the line of vision may be turned by a voluntary effort varies in different individuals, even when the eyes are perfectly normal. In myopic eyes, the centre of rotation is deeper in the orbit than normal, and the extent of the possible deviation of the visual line is correspondingly diminished. Helmholtz states that, in his own person, with the greatest effort that he is capable of making, he can move the line of vision in the horizontal plane to the extent of about fifty degrees, and, in the vertical plane, about forty-five degrees; but he adds that these extreme rotations are very forced, and that they cannot be sustained for any length of time.[1] It is probable that we seldom move the eyeball in any direction to an angle of forty-five degrees, the direction of the visual line being more easily accomplished by movements of the head.

Action of the Recti Muscles.—The action of the recti, particularly the internal and external, is quite simple.

The internal and the external recti rotate the globe upon a vertical axis, which is perpendicular to the axis of the eye. The isolated action of these muscles, particularly the external rectus, is often illustrated in certain forms of paralysis, which have been alluded to in connection with the history of the cranial nerves.[2]

The superior and the inferior recti rotate the globe upon an horizontal axis, which is not at right angles with the axis of the eye, but is inclined from the nasal side slightly backward. The line which serves as the axis of rotation for these muscles forms an angle of about seventy degrees with the axis of the globe;[3] and, as a consequence of this arrangement, their action is not so simple as that of the internal and external recti. The insertion of the superior rectus is such,

[1] Helmholtz, *Optique physiologique*, Paris, 1867, p. 598.

[2] For an account of the effects of paralysis of one or more of the nerves of the eyeball, the reader is referred to vol. iv., Nervous System, p. 128, *et seq.*

[3] Helmholtz, *op. cit.*, p. 40.

that when it contracts, the pupil is directed upward and inward, the inferior rectus directing the pupil downward and inward.

The above represents the simple, isolated action of each pair of recti muscles; but it is easy to see how, without necessarily involving the action of the oblique muscles, the globe may be made to perform an immense variety of rotations, and the line of vision may be turned in nearly every direction, by the action of the recti muscles alone.

Action of the Oblique Muscles.—Although there has been considerable discussion concerning the exact mode of action of the oblique muscles, their mechanism may now be regarded as pretty well settled, at least as regards the human subject. In the first place, it is sufficient for all practical purposes, to assume that the superior and the inferior oblique muscles act as direct antagonists to each other. The next point to determine is the direction of the axis of rotation of the globe with reference to the action of these muscles. The most exact, recent measurements show that this axis is horizontal, and that it has an oblique direction, from before backward and from without inward. The angle formed by the axis of rotation of the oblique muscles with the axis of the globe is thirty-five degrees; and the angle between the axis of the oblique muscles and the axis of the superior and inferior recti muscles is seventy-five degrees.[1]

Given the direction of the axis of rotation and the direction of the superior oblique muscle, it is easy to understand the effects of its contraction. As this muscle, passing obliquely backward and forward over the globe, acts from the pulley near the inner angle of the eye to its insertion just behind the anterior half of the globe on its external and superior surface (see Fig. 8), it must rotate the globe so as to direct the pupil downward and outward.

The inferior oblique, passing outward and slightly back-

[1] Helmholtz, *Optique physiologique*, Paris, 1867, p. 41.

ward under the globe, acts from its origin at the margin of the orbit near the inner angle of the eye to its insertion, which is just below the insertion of the superior oblique. This muscle rotates the globe so as to direct the pupil upward and outward.

The action of the oblique muscles seems to be specially connected with the movements of torsion of the globe.[1] It is necessary to distinct, single vision with both eyes, that the images should be formed upon exactly corresponding points on the retina, and that they should bear, for the two eyes, corresponding relations to the perpendicular. Thus it is that, when the head is inclined to one side, the eyes are twisted upon an oblique, antero-posterior axis, as can be readily observed if we watch little spots upon the iris during these movements.

The superior oblique muscle is supplied by a single nerve, the patheticus. When this muscle is paralyzed, the inferior oblique acts without its antagonist, and the eyeball is immovable, as far as the twisting of the globe, just described, is concerned. When the head is moved toward the shoulder, the globe cannot rotate to maintain a position corresponding to that of the other eye, and we have double vision. This point has already been touched upon in connection with the physiology of the nerves of the eyeball[2] and the discussion of the corresponding points in the retina.[3]

Associated Action of the Different Muscles of the Eyeball.—It is almost unnecessary to add, after the description just given of the actions of the individual muscles of the globe, that their contractions may be associated, so as to pro-

[1] We use the word torsion in a sense different from that of rotation. By torsion, we mean the twisting of the eyeball upon the axis of the oblique muscles, as a wheel would turn upon an axle, maintaining, in this way, a constant and exact relation, for the two eyes, between the vertical and the horizontal meridian. We make this explanation for the reason that torsion is a word not commonly used by English writers. It corresponds to *Raddrehung*, in German.

[2] See vol. iv., Nervous System, p. 186. [3] See page 119.

duce an infinite variety of movements. We have no consciousness, under ordinary circumstances, of the muscular action by which the globe is rotated and twisted in various directions, except that, by an effort of the will, we direct the visual line toward different objects. By a strong effort, we can make the eyes converge by contracting both internal recti, and some persons can produce extreme divergence by using both external recti; but this is abnormal.

In looking at distant objects, the axes of vision are practically parallel. When we look at near objects, the effort of accommodation is attended with the amount of convergence necessary to bring the visual axes to bear upon identical points. In looking around at different objects, we move the head more or less, rotating and twisting the globes in various directions. In the movements of the globes vertically, the axes are kept parallel, or at the proper angle, by the internal and external recti, and the superior and inferior recti upon the two sides act together. In rotating the globe from one side to the other, upon a vertical axis, the external rectus upon one side acts with the internal rectus upon the other. In the movements of torsion upon an antero-posterior axis, there must be an associated action of the oblique muscles and the recti. We quote from Longet the following, as illustrative of this combination of action:

"If the eyes be directed obliquely upward and to the left, the vertical meridians of the two eyes are parallel and inclined from left to right, for the left eye, outward, and for the right eye, inward. The movement of the left eye upward and to the left, or outward, necessitates a contraction of the superior rectus, the external rectus, and the inferior oblique muscles. As regards the right eye, also directed upward and to the left, that is to say, inward, this is moved by the simultaneous action of the superior rectus, the internal rectus, and the inferior oblique."[1]

We have given the above quotation simply to illustrate a

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome ii., p. 928.

combination of action of three muscles for each eye, the only difference in binocular vision being that in one eye the external rectus is brought into play, while the internal rectus acts upon the opposite side. Reversing this action of the internal and external recti, we have the action which directs the pupil upward and to the right. If we substitute for the superior rectus and the inferior oblique, the inferior rectus and the superior oblique, we have the pupil directed downward, and either to the right or left, as the internal or external rectus upon either side is brought into action.

One important point, never to be lost sight of in our study of the associated action of the muscles of the globe, relates to the combined movements of the two eyes. We have already seen that perfect binocular vision is possible only when impressions are made upon exactly corresponding points in the retina of each eye.[1] If one eye be deviated in the horizontal plane, the points no longer correspond, and there is double vision, the same as if two impressions were made upon one retina; for when the impressions exactly correspond, the two retinæ act practically as a single organ. The same is true in deviation of the globe in the vertical plane. If we suppose, for sake of argument, that the retina is square, it is evident that a torsion, or twisting of one globe upon an antero-posterior axis (*Raddrehung*) must be attended with an analogous movement of the other globe, in order to bring the visual rays to bear upon the corresponding points; in other words, the obliquity of the assumed square of the retina must be exactly the same for the two eyes, or the coincidence of the corresponding points would be disturbed, and we should have double vision. When we clearly understand that deviation of one eye in the horizontal or the vertical plane disturbs the relation of the corresponding points, which is sufficiently easy of comprehension, and that a deviation from exact coincidence of action in torsion of the globes, twists, as it were, the corresponding points, so that their rela-

[1] See page 119.

tion is also disturbed, we can see that the varied movements of the globes, by the combined action of the recti and oblique muscles, must correspond for each eye, in the movements of torsion upon an antero-posterior axis, as well as in movements of rotation upon the horizontal or the vertical axis.

We cannot go more elaborately into the various combinations of action of the muscles of the eyeball, without giving the subject more prominence than is desirable in a general treatise on physiology. These questions are minutely studied by Helmholtz, in the work to which we have so often referred.[1]

Parts for the Protection of the Eyeball.

The orbit, formed by the union of certain of the bones of the face, receives the eyeball, the ocular muscles, the muscle of the upper lid, blood-vessels, nerves, part of the lachrymal apparatus, and contains, also, a certain amount of adipose tissue, which latter never disappears, even in extreme marasmus. The bony walls of this cavity protect the globe and lodge the parts above enumerated. The internal, or nasal wall of the orbit projects considerably beyond the external wall, so that the extent of vision is far greater in the outward than in the inward direction. As the globe is more exposed to accidental injury from an outward direction, the external wall of the orbit is strong, while the bones which form its internal wall are comparatively fragile. The upper semicircumference of the orbit, the superciliary ridge, is provided with short, stiff hairs, the eyebrows, which serve to shade the eye from excessive light and to protect the eyelids from perspiration from the forehead.

The eyelids are folds of very thin integument, lined by a mucous membrane, the conjunctiva. The subcutaneous connective tissue is thin and loose, and is entirely free from fat. It presents numerous short papillæ and small sudoriparous glands. At the borders of the lids, are short, stiff, curved hairs, arranged in two or more rows, the eyelashes, or cilia.

[1] HELMHOLTZ, *Optique physiologique*, Paris, 1867.

Those of the upper lid are longer and more numerous than the lower cilia. The curve of the lashes is from the eyeball. They serve to protect the globe from dust, and, to a certain extent, to shade the eye.

The tarsal cartilages are small, elongated, semilunar plates, extending from the edges of the lids toward the margin of the orbit. Their length is about an inch. The central portion of the upper cartilage is about one-third of an inch broad, and the corresponding portion of the lower cartilage measures about one-sixth of an inch. At the inner canthus of the eye, is a small, delicate ligament, or tendon, the tendo palpebrarum, which is attached to the lachrymal groove internally, passes outward, and divides into two lamellæ, which are attached to the two tarsal cartilages. At the outer canthus, the cartilages are attached to the malar bone by the external tarsal ligament. The tarsal cartilages receive an additional support from the palpebral ligament, a fibrous membrane, attached to the margin of the orbit and the convex border of the cartilages, and lying beneath the orbicularis muscle. This membrane is strongest near the outer angle of the eye.

On the posterior surface of the tarsal cartilages, partly embedded in them and lying just beneath the conjunctiva, are the Meibomian glands. The structure and functions of these glands have already been considered in connection with secretion.[1] They produce an oily fluid, which smears the edges of the eyelids and prevents the overflow of tears.

Muscles which open and close the Eyelids.—Leaving out the corrugator supercilii, which draws the skin of the forehead downward and inward, we have the orbicularis palpebrarum, which closes the lids, and the levator palpebræ superioris, which raises the upper lid. The tensor tarsi, called the muscle of Horner, is a very thin, delicate muscle, which is little more than a deep portion of the orbicularis. Con-

[1] See vol. iii., Secretion, p. 62.

sidering this as a distinct muscle, it consists of two delicate slips, which pass from either eyelid behind the lachrymal sac, uniting here to go to its attachment at the posterior portion of the lachrymal bone. When this acts with the orbicularis, it compresses the lachrymal sac.

The orbicularis palpebrarum is a broad, thin muscle, closely attached to the skin, surrounding the free margin of the lids, and extending a short distance over the bones, beyond the margin of the orbit. This muscle may be described as arising from the tendo palpebrarum, the surface of the nasal process of the superior maxillary bone, and the internal angular process of the os frontis. From this origin at the inner angle of the eye, its fibres pass elliptically around the fissure of the lids, as above indicated. Its action is to close the lids. In the ordinary, moderate contraction of this muscle, only the upper lid is moved; but, in forcible contraction, the lower lid moves slightly and the lids are drawn toward the nose. In facial palsy, or when the temporo-facial branch of the portio dura of the seventh nerve is paralyzed, this muscle cannot act, and it is impossible to close the eye.

The levator palpebræ superioris is situated within the orbit. It arises from a point a little above and in front of the optic foramen at the apex of the orbit, passes forward above the eyeball, and spreads into a thin tendon, which is inserted into the anterior surface of the superior tarsal cartilage. Its evident action is to raise the upper lid. It is animated by filaments from the third pair of cranial nerves; and, when this nerve is paralyzed, we have permanent falling of the upper lid, or blepharoptosis. This muscle and its relations are shown in Fig. 8, page 131.

In the act of opening the eyes, the levator muscles alone are brought into play. Closing of the lids is accomplished by the orbicular muscles. Both of these sets of muscles act to a great extent without the intervention of the will. The eyes are kept open almost involuntarily, except in extreme fatigue; though, when the will ceases to act, the lids are

closed. Nevertheless we are hardly conscious of an effort in keeping the eyes open, in our waking moments, and we require an effort to close the eyes. During sleep, the eyes are closed and the globes are turned upward. The contractions of the orbicular muscles which take place in winking are usually involuntary. This act occurs at short intervals, and is useful in spreading the lachrymal secretion over the exposed portions of the globes. The action of both sets of muscles is usually symmetrical, though we may educate them so as to close one eye while the other is kept open. The action of the orbicularis is so far removed from the control of the will, that when the surface of the globe is touched or irritated, or when the impression of light produces intense pain, it is impossible to keep the eye open.

Conjunctival Mucous Membrane.—The entire inner surface of the upper and lower eyelids is lined by a mucous membrane, which is reflected forward from the inner periphery of the lids over the eyeball. The membrane lining the lids is called the palpebral conjunctiva, and that covering the eyeball, the ocular conjunctiva. The latter presents a sclerotic and a corneal portion. The membrane presents a superior and an inferior fold, where it is reflected upon the globe. In the superior conjunctival fold, are numerous glandular follicles, or accessory lachrymal glands, which secrete a certain portion of the fluid which moistens the surface of the eyeball. These are generally described as forming a portion of the lachrymal gland. At the inner canthus, there is a vertical fold, the plica semilunaris, with a reddish, spongy elevation at its inner portion, called the caruncula lacrymalis. The caruncula presents a collection of follicular glands, with a few delicate hairs on its surface. The conjunctiva is continuous with the membrane of the lachrymal ducts, the puncta lacrymalia, and the Meibomian glands. Beneath the conjunctiva, except in the corneal portion, is a loose connective tissue.

The palpebral conjunctiva is reddish, thicker than the

ocular portion, furrowed, and presents small, isolated papillæ near the borders of the lids, which increase in number and size toward the folds. This portion of the membrane presents large capillary blood-vessels and lymphatics, and is covered with a layer of cells of flattened epithelium. The sclerotic portion is thinner, less vascular, and has no papillæ. It is covered by conical and rounded epithelial cells, which present from two to four layers. Over the cornea, the epithelium of the sclerotic portion is continued in delicate, transparent layers, without a distinct basement membrane.

The nerves of the ocular portion of the conjunctiva and the folds have a peculiar termination in simple bulbs, observed by Krause, which have already been described.[1] This appearance of bulbs is thought by some to be artificial and due to extravasation of myeline in making the preparations; but they are regarded as true bulbs by many high authorities.[2]

The Lachrymal Apparatus.—The eyeball is constantly bathed in a thin, watery fluid which is secreted by the lachrymal gland, is spread over the globe by the movements of the lids and of the eyeball, and is prevented, under ordinary conditions, from overflowing upon the cheek, by the Meibomian secretion. The excess of this fluid is collected into the lachrymal sac and is carried into the nose by the nasal duct. The lachrymal gland, the lachrymal canals, duct, and sac, and the nasal duct, constitute the lachrymal apparatus.

The lachrymal gland is an ovoid, flattened gland of the racemose variety, resembling the salivary glands in its general structure. It is about the size of a small almond, and is lodged in a shallow depression in the bones of the orbit at its upper and outer portion. It is closely attached to the perios-

[1] See vol. iv., Nervous System, p. 42.

[2] STRICKER, *Manual of Human and Comparative Histology*, The New Sydenham Society, London, 1873, vol. iii., p. 453, *et seq.*

teum by its upper surface, and is moulded below to the convexity of the globe. Its anterior portion is separated from the rest by a well-marked groove, is comparatively thin, and adheres to the upper lid. It presents from six to eight, usually seven, ducts, which form a row of openings into the conjunctival fold. Five or six of these orifices are situated above the outer canthus and two or three open below. In its minute structure, this gland presents no points of special physiological interest as distinguished from the ordinary racemose glands. It receives nervous filaments from the fifth cranial nerve and the sympathetic.

The apparatus by which the excess of tears is conducted into the nose begins by two little points, situated on the margin of the upper and the lower lid, near the inner canthus, called the puncta lacrymalia, which present each a minute orifice. These points lead respectively into the upper and the lower lachrymal canals, which together surround the caruncula lacrymalis. At the inner angle, just beyond the caruncula, the two canals join, to empty into the lachrymal sac, which is the dilated upper extremity of the nasal duct. The duct is about half an inch in length, and empties into the inferior meatus of the nose, taking a direction nearly vertical, inclined slightly outward and backward. This portion of the lachrymal apparatus is fibrous and is lined by a reddish mucous membrane, which presents several well-marked folds. Near the puncta, are two folds, one for each lachrymal canal. Another pair of folds exists near the horizontal portions of the canals. At the opening of the duct into the nose, is an overhanging fold of the nasal mucous membrane. These folds are supposed to prevent the reflux of fluid from the lachrymal canals and the entrance of air from the nose. The mucous membrane of the lachrymal canals is covered by a flattened epithelium, like that of the conjunctiva. The lachrymal sac and duct are lined by a continuation of the ciliated epithelium of the nose. The disposition of the apparatus just described is shown in Fig. 9.

The Tears.—The secretion of the lachrymal glands is constant, though the quantity of fluid may be increased under various conditions. The actual amount of the secretion has never been estimated. During sleep, it is much diminished; and, when the eyes are open, the quantity is just sufficient to moisten the eyeball, the excess being carried into the nose so gradually that this process is not appreciated. That this drainage of the excess of tears takes place is shown by cases of obstruction of the nasal duct, when the liquid constantly overflows upon the cheeks, producing considerable inconvenience.

FIG. 9.

Lachrymal canals, lachrymal sac, and nasal canal, opened by their anterior portion.—1, walls of the lachrymal passages, smooth and adherent; 2, 2, walls of the lachrymal sac, presenting delicate folds of the mucous membrane; 3, a similar fold belonging to the nasal mucous membrane. (SAPPEY, *Traité d'anatomie*, Paris, 1871, tome iii., p. 708.)

The mechanism of the action of the excretory lachrymal apparatus is quite simple, though it has been the subject of a good deal of discussion. It is probable that the openings at the puncta lacrymalia take up the liquid like delicate pipettes, this action being aided by the movements in winking, by which, when the lids are closed, the points are compressed and turned backward, opening and drawing in the tears when the lids are opened. It is possible that the lachrymal sac is compressed in the act of winking, by the contractions of the muscle of Horner, and that this, while it empties the sac, may, in the subsequent relaxation, assist the introduction of liquid from the orbit.

We know very little with regard to the chemical composition of the tears, beyond the analysis made many years ago by Frerichs. According to this observer, the following is the composition of the lachrymal secretion:

Composition of the Tears.[1]

Water	990·60	to	987·00
Epithelium	1·40	"	3·20
Albumen	0·80	"	1·00
Chloride of sodium, Alkaline phosphates, Earthy phosphates, Mucus, Fat,	7·20	"	8·80
	1000·00		1000·00

The specific gravity of the tears has never been ascertained. The liquid is perfectly clear, colorless, of a saltish taste and a feebly alkaline reaction. The albumen given in the table is called by some authors, lachrymine, thrænine, or dacryoline.[2] This substance, whatever it may be called, resembles mucus in many regards, and is probably secreted by the conjunctiva and not by the lachrymal glands. It differs from ordinary mucus in being coagulated by water.[3]

The secretion of tears is readily influenced through the nervous system. Aside from the increased flow of this secretion from emotional causes, which probably operate through the sympathetic, a hypersecretion almost immediately follows irritation of the mucous membrane of the conjunctiva or of the nose. The same result follows violent muscular effort, laughing, coughing, sneezing, etc. The secretion of tears under stimulation of the mucous membrane is reflex. A number of years ago, Magendie transfixed with a needle the lachrymal nerve in a man, and passed through it a feeble galvanic current, producing an excessive flow of tears.[4] The action in this case was undoubtedly reflex.

[1] Frerichs, *Thränensecretion*, in Wagner, *Handwörterbuch der Physiologie*, Braunschweig, 1846, Bd. iii., Erste Abtheilung, S. 618.

[2] Robin et Verdeil, *Chimie anatomique*, Paris, 1853, tome iii., p. 452.

[3] See vol. iii., Secretion, p. 56.

[4] Magendie, *Précis élémentaire de physiologie*, Paris, 1836, tome i., p. 59, note.

CHAPTER VII.

AUDITORY NERVES—TOPOGRAPHICAL ANATOMY OF THE EAR.

Physiological anatomy of the auditory nerves—General properties of the auditory nerves—Effects of galvanic currents passed through the ear—Topographical anatomy of the parts essential to the appreciation of sound—The external ear—General arrangement of the parts composing the middle ear—Anatomy of the tympanum—Arrangement of the ossicles of the ear—Muscles of the middle ear—Mastoid cells—Eustachian tube—Muscles of the Eustachian tube—Mucous membrane of the middle ear and of the Eustachian tube—General arrangement of the bony labyrinth.

The general considerations introductory to the study of vision are equally applicable to the physiology of hearing. The impressions of sound are conveyed to the brain by special nerves; but, in order that these impressions shall reach these nerves so as to be properly appreciated, a complex accessory apparatus is required, the integrity of which is essential to perfect audition. The study of the arrangement and action of these accessory parts is even more important and is far more intricate than the study of the auditory nerves. The latter simply convey the impressions to the brain, by a mechanism analogous to that of general nervous conduction, the essential character of which is not fully understood. The auditory nerves conduct impressions of sound, as the optic nerves conduct impressions of light; and this statement expresses the extent of our positive knowledge; but there is an elaborate apparatus by which the waves are collected, conveyed to a membrane capable of vibration, and finally carried to the nerves, by which we are enabled to appreciate the intensity and the varied qualities of sound.

Our positive and definite knowledge of the auditory ap-

paratus is by no means so complete as it is with regard to the eye, nor do we as yet understand so clearly the physiological relations of many points developed by late anatomical researches; and, for this reason, it does not seem desirable to consider the structure of the ear as fully as we have the anatomy of the eye, restricting ourselves, as we have done, to the physiological anatomy of parts. With this end in view, we shall take up fully the following points:

1. The physiological anatomy and the general properties of the auditory nerves

2. The physiological anatomy of the parts essential to the correct appreciation of sound.

3. The laws of the propagation of sonorous vibrations, as far as they are applicable to audition.

4. The physiological action of different parts of the auditory apparatus.

Physiological Anatomy of the Auditory Nerves.—The auditory nerve constitutes the portio mollis of the seventh pair of Willis. The origin of this nerve can easily be traced to the floor of the fourth ventricle, where it presents two roots. The external, or superficial root, sometimes called the posterior root, can be seen usually without preparation. This consists of from five to seven grayish filaments, which decussate in the median line, and pass outward, winding from the fourth ventricle around the restiform body. The deep root consists of numerous distinct filaments, arising from the gray matter of the fourth ventricle, two or three of which pass to the median line to decussate with corresponding filaments of the opposite side. This root passes around the restiform oody inward, so that this portion of the medulla is encircled, as it were, by the two roots. Passing from the superior and lateral portion of the medulla oblongata, the trunk of the nerve is applied to the superior and anterior surface of the facial. It then passes around the middle peduncle of the cerebellum, and receives a process from the arachnoid mem-

brane, which envelops it in a common sheath with the facial. It then penetrates the internal auditory meatus. In its course, it receives filaments from the restiform body, and possibly from the pons Varolii. Within the meatus, the nerve divides into an anterior and a posterior branch, the anterior being distributed to the cochlea, and the posterior, to the vestibule and semicircular canals. The distribution of these branches will be fully described in connection with the anatomy of the internal ear.

The color of the auditory nerve is grayish, and its consistence is soft, thus differing from the ordinary cerebro-spinal nerves, and resembling, to a certain extent, the other nerves of special sense. On the external, or superficial root, is a small ganglioform enlargement, containing fusiform nerve-cells. According to the latest researches, the filaments of the trunk of this nerve consist of very large axis-cylinders, surrounded by a medullary sheath, but having no tubular membrane. In the course of these fibres, are found small, nucleated ganglionic enlargements.[1]

General Properties of the Auditory Nerves.—There can be no doubt, as regards the portio mollis of the seventh, that it is the only nerve capable of receiving and conveying to the brain the special impressions produced by waves of sound; but it is an interesting question to determine, whether this nerve be endowed also with general sensibility. Analogy with most of the other nerves of special sense would indicate that the auditory nerves are insensible to ordinary impressions; and this view is sustained by direct experiments, made many years ago. Magendie exposed, in a rabbit, the trunk of the fifth, and the auditory nerve, "and, whenever the fifth pair was touched as lightly as possible, there was evidence of the most acute sensibility, while the animal was passive when the auditory was touched, pressed, or even

[1] WALDEYER, in STRICKER, *Manual of Human and Comparative Histology*, The New Sydenham Society, London, 1873, vol. iii., p. 169.

torn."[1] Analogous observations have been made by Valentin[2] and by Schiff;[3] but, in opposition to these, is a statement by Brown-Séquard, that the degree of pain produced by excitation of the auditory nerve "appears to be as considerable as that caused by a similar excitation of the trigeminal nerve."[4] This bare assertion, however, we can hardly accept in opposition to the clear results of previous experiments and the analogy with observations upon the other nerves of special sense.

The phenomena observed during the passage of galvanic currents through the auditory nerves have, of late years, been the subject of much discussion. The old experiment of Volta,[5] which was almost immediately confirmed by Ritter,[6] is sufficiently familiar, and is often quoted as showing that galvanic stimulation of these nerves produces a sensation of sound; but the facts ascertained leave room for doubt with regard to the precise mode of action of the current. A careful study of recent observations on this point renders the question even more obscure; but, from a purely physiological point of view, we have only to do with the effects of stimulating the auditory nerves in health. Leaving the therapeutic and diagnostic uses of galvanism out of the question, we find that there is considerable uncertainty with regard to the fact of direct stimulation of the auditory nerves, in the recent experiments with the galvanic current. Brenner observed strong sensations of sound with one of the poles of a battery in the auditory passage filled with water

[1] MAGENDIE, *Suite des expériences sur les fonctions de la cinquième paire de nerfs.—Journal de physiologie*, Paris, 1824, tome iv., p. 314.

[2] VALENTIN, *Lehrbuch der Physiologie*, Braunschweig, 1844, Bd. ii., S. 678.

[3] SCHIFF, *Lehrbuch der Physiologie*, Lahr, 1858–'59, Bd. i., S. 399.

[4] BROWN-SÉQUARD, *Experimental Researches applied to Physiology and Pathology*, New York, 1858, p. 100.

[5] VOLTA, *On the Electricity excited by the mere Contact of conducting Substances of different kinds.—Philosophical Transactions*, London, 1800, p. 427.

[6] RITTER, *Versuche und Bemerkungen über den Galvanismus der Voltaischen Batterie.—Annalen der Physik*, Halle, 1801, Bd. vii., S. 468, *et seq.*

and the other connected with different parts of the body.[1] When the cathode was placed in the ear, the sound was heard at the making of the current. With the anode in the ear, there was no sound at the making of the current or during its passage, but a slight sound was heard at the breaking of the current. These phenomena closely resemble those produced by the galvanic current applied to ordinary motor nerves, in so far as the action seemed to be most vigorous at the making of the circuit, with the direct current, and at the breaking of the circuit, with the inverse current; for, when the cathode is placed in the ear, the current is direct, following the course of the nerve from the centre to the periphery, and *vice versa*. In view of the fact that some writers attribute the subjective auditory phenomena observed by Brenner to stimulation of branches of the facial, and, through this nerve, to the action of the muscles of the middle ear, it is interesting, in this connection, to refer to the experiments of Chauveau upon the action of the direct and the inverse current upon the facial.[2] Without following out the discussion of this question in detail, it seems only necessary to study the very clear and satisfactory experiments of Wreden, to become convinced that the subjective auditory phenomena, attributed by Brenner and others to irritation of the auditory nerves, are due to contraction of the muscles of the middle ear, particularly the stapedius. The facts, clinical and experimental, upon which this view is based, are the following: In cases of clonic spasm of the stapedius, sensations of sound have been observed, exactly like those produced by an induced current. In cases of complete facial paralysis from otitis, in which paralysis of the auditory nerve could be positively excluded, it was not possible to produce subjective auditory sensations, even by powerful galvanization by a catho-

[1] BRENNER, *Zur Elektrophysiologie und Elektropathologie des Nervus acusticus.*—*St. Petersburger medicinische Zeitschrift*, St. Petersburg, 1868, Bd. iv., S. 286, *et seq.*

[2] See vol. iv., Nervous System, p. 110.

ter passed through the Eustachian tube into the tympanic cavity, or by the external meatus. In addition, there are other well-established clinical observations, mentioned by Wreden, which sustain the theory of muscular contraction, and are opposed to the idea of direct stimulation of the auditory nerves.[1]

The facts just stated show that there is no positive evidence of the production of impressions of sound by galvanic stimulation of the auditory nerves; while it appears, from experiments which we have already cited, that these nerves are not endowed with general sensibility. The results, then, as regards the auditory nerves, are simply negative. Were it possible to expose these nerves to mechanical or galvanic stimulation, in the human subject, without involving other parts, we might arrive at some definite conclusion; but the difficulties in the way of such an experiment, it must be admitted, have thus far proved insurmountable.

Topographical Anatomy of the Parts essential to the Appreciation of Sound.

Perfect audition requires the anatomical integrity of a very complex apparatus, which, for convenience of anatomical description, may be divided into the external, middle, and internal ear. A correct appreciation of the physiology of these parts demands, as a necessary preparation, a knowledge of their physiological anatomy:

1. The external ear includes the pinna and the external

[1] WREDEN, *Beiträge zur Begründung einer Lehre über die elektrische Reizung der Binnenmuskeln des Ohres.—St. Petersburger medicinische Zeitschrift*, St. Petersburg, 1871, Neue Folge, Bd. ii., S. 440.

A very full review of the literature of this subject, with copious references, is given by Wreden (*Ein Fall von Verbrennung der Paukenhöhle*, etc.—*St. Petersburger medicinische Zeitschrift*, St. Petersburg, 1871, Neue Folge, Bd. i., Separatabdruck, S. 86, *et seq.*) A reply, by Schwartze, to the experiments and conclusions of Brenner is published in the *Archiv für Ohrenheilkunde*, Würtzburg, 1864, Bd. i., S. 44, *et seq.*; and a review of Brenner's theory and the reply of Schwartze was published by Hagen, in 1866. (*Praktische Beiträge zur Ohrenheilkunde*, Leipzig, 1866.)

auditory meatus, which is closed internally by the membrana tympani.

2. The middle ear includes the cavity of the tympanum, or drum, with its boundaries. The parts here to be described are, the membrana tympani, the form of the tympanic cavity, its openings, its lining membrane, and the small bones of the ear, or ossicles, with their ligaments, muscles, and nerves. The cavity of the tympanum communicates, by the Eustachian tube, with the pharynx and also presents openings into the mastoid cells.

3. The internal ear contains the terminal filaments of the auditory nerve. It includes the vestibule, the three semicircular canals, and the cochlea, which together form the labyrinth.

The pinna and the external meatus simply conduct the waves of sound to the tympanum. The parts entering into the structure of the middle ear are accessory, and are analogous, in their functions, to the refracting media of the eye. Structures contained in the labyrinth constitute the true sensory organ; and these bear the same relations to the auditory apparatus as the retina to the eye.

The External Ear.—It is hardly necessary to our purpose to describe very minutely the external ear. The pinna, or auricle, is that portion projecting from the head, which first receives the waves of sound. Beginning externally, we have the helix, which is the outer ridge of the pinna. Just within this, is a groove, called the fossa of the helix. This fossa is bounded anteriorly by a prominent but shorter ridge, called the antihelix; and above the concha, between the superior portion of the antihelix and the anterior portion of the helix, is a shallow fossa, called the fossa of the antihelix. The deep fossa, immediately surrounding the opening of the meatus, is called the concha. A small lobe projects posteriorly, covering the anterior portion of the concha, and is called the tragus; and the projection at the lower ex-

tremity of the antihelix is called the antitragus. The fleshy, dependent portion of the pinna is called the lobule of the ear.

The form of the pinna and its consistence depend upon the presence of fibro-cartilage, which occupies the whole of the external ear except the lobule. This structure has already been described in another volume.[1]

The integument covering the ear does not vary much from the integument of the general surface. It is thin, closely attached to the subjacent parts, and possesses small, rudimentary hairs, with sudoriparous and sebaceous glands.

The muscles of the ear are not important in the human subject; and, excluding a few exceptional cases, they are not under the control of the will. The extrinsic muscles are the superior, or attolens, the anterior, or attrahens, and the posterior, or retrahens auri. In addition, there are the six small intrinsic muscles, situated between the ridges upon the cartilaginous surface. The pinna is attached to the sides of the head by two distinct ligaments and a few delicate ligamentous fibres.

The external auditory meatus is about an inch and a quarter in length, and extends from the concha to the membrana tympani. Its course is somewhat tortuous. Passing from without inward, its direction is at first somewhat upward, turning abruptly over a bony prominence near the middle, from which it has a slightly downward direction to the membrana tympani. Its general course is from without inward and slightly forward. The inner termination of the canal is the membrana tympani, which is quite oblique, the upper portion being inclined outward, so that the inferior wall of the meatus is considerably longer than the superior.

The walls of the external meatus are partly cartilaginous and fibrous, and partly bony. The cartilaginous and fibrous portion occupies a little less than half of the entire length, and consists of a continuation of the cartilage of the pinna with fibrous tissue. About the lower two-thirds of this por-

[1] See vol. iii., Movements, p. 488.

tion of the canal is cartilaginous, the upper third being fibrous. The rest of the tube is osseous, and is a little longer and narrower than the cartilaginous portion. Around the inner extremity of the canal, with the exception of its superior portion, is a narrow groove, which receives the greater portion of the margin of the membrana tympani.

The skin of the external meatus is continuous with the integument covering the pinna. It is very delicate, becoming thinner from without inward. In the osseous portion, it adheres very closely to the periosteum, and, at the bottom of the canal, it is reflected over the membrana tympani, forming its outer layer. In the cartilaginous and fibrous portion, are numerous short, stiff hairs, with sebaceous glands attached to their follicles, and the coiled tubes known as the ceruminous glands. The structure of these glands and the properties and composition of the cerumen have already been described under the head of secretion.[1]

General Arrangement of the Parts composing the Middle Ear.—Without a very elaborate and minute anatomical description, fully illustrated by plates, it is difficult to give a clear idea of the structure and relations of the very complex apparatus of the middle and the internal ear. Such a minute and purely anatomical description would be out of place in this work, where it is desired only to give such an account of the anatomy as will enable the student to comprehend the physiology of the ear, reserving for special description certain of the most important structures. In beginning the difficult task of describing the physiological anatomy of the middle and internal ear, it will be convenient to give a general outline of the different parts, with their names. This, with a careful study of Figs. 10, 11, 12, and 13, can hardly fail to greatly facilitate the closer investigation of the more important structures.

The arrangement of the parts constituting the external

[1] See vol. iii., Secretion, pp. 60, 69.

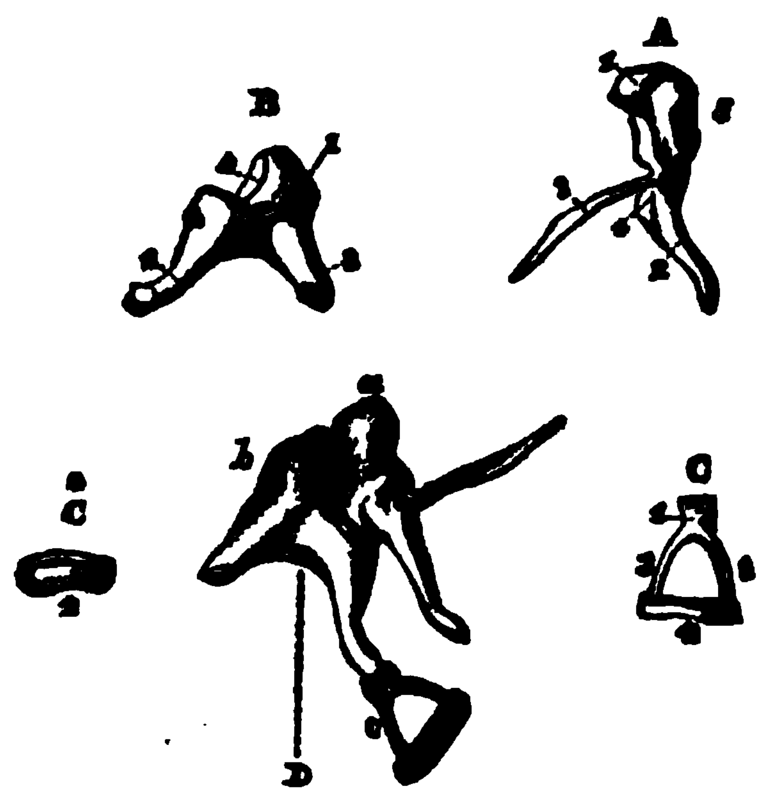
ear is sufficiently simple. The middle ear presents a narrow cavity, Fig. 10, (11), of irregular shape, situated between the external ear and the labyrinth, in the substance of the temporal bone. The general arrangement of its parts is shown in Fig. 10. The outer wall of the tympanic cavity is formed by the membrana tympani, Fig. 10, (6). This membrane is concave, its concavity looking outward, and oblique, inclining usually at an angle of about forty-five degrees with the perpendicular. This angle, however, varies considerably in different individuals. The roof is formed by an exceedingly

FIG. 10.

General view of the organ of hearing.—1, pinna; 2, cavity of the concha, on the walls of which are seen the orifices of a great number of sebaceous glands; 3, external auditory meatus; 4, angular projection formed by the union of the anterior portion of the concha with the posterior wall of the auditory canal; 5, openings of the ceruminous glands, the most internal of which form a curved line which corresponds with the beginning of the osseous portion of the external meatus; 6, membrana tympani and the elastic fibrous membrane which forms its border; 7, anterior portion of the incus; 8, malleus; 9, handle of the malleus applied to the internal surface of the membrana tympani, which it draws inward toward the projection of the promontory; 10, tensor-tympani muscle, the tendon of which is reflected at a right angle to become attached to the superior portion of the handle of the malleus; 11, tympanic cavity; 12, Eustachian tube, the internal, or pharyngeal extremity of which has been removed by a section perpendicular to its curve; 13, superior semicircular canal; 14, posterior semicircular canal; 15, external semicircular canal; 16, cochlea, 17, internal auditory canal; 18, facial nerve; 19, large petrosal branch, given off from the ganglioform enlargement of the facial and passing below the cochlea to go to its distribution; 20, vestibular branch of the auditory nerve; 21, cochlear branch of the auditory nerve. (SAPPEY, *Traité d'anatomie*, Paris, 1871, tome iii., p. 503.)

thin plate of bone. The floor is bony, and is much narrower than the roof. The inner wall, separating the tympanic cavity from the labyrinth, is irregular, presenting several small elevations and foramina. The fenestra ovalis, an ovoid opening near its upper portion, leads to the cavity of the vestibule. This is closed, in the natural state, by the base of the stapes and its annular ligament. Below, is a smaller,

FIG. 11.



Bones of the tympanum of the right side (from Arnold).—A, malleus; 1, its head; 2, the handle; 3, long, or slender process; 4, short process; B, incus; 1, its body; 2, the long process with the orbicular process; 3, short, or posterior process; 4, articular surface receiving the head of the malleus; C, stapes; 1, head; 2, posterior crus; 3, anterior crus; 4, base; C*, base of the stapes; D, the three bones in their natural connection as seen from the outside; *a*, malleus; *b*, incus; *c*, stapes. (QUAIN, *Elements of Anatomy*, London, 1867, vol. ii., p. 748.)

ovoid opening, the fenestra rotunda, which leads to the cochlea. This is closed, in the natural state, by a membrane, called the secondary membrana tympani. In addition, the posterior wall presents several small foramina leading to the mastoid cells, which are lined by a continuation of the mucous membrane of the tympanic cavity. The tympanic cavity also presents an opening leading to the Eustachian tube, and a small foramen, which gives passage to the tendon of the stapedius muscle. The Eustachian tube extends from the upper part of the pharynx to the tympanum.

The small bones of the ear are three in number;[1] the incus, the malleus, and the stapes, forming a chain, connected together by ligaments (Fig. 11). These bones are situated in the upper part of the tympanic cavity. The handle of the malleus (A, 2, Fig. 11) is closely attached to the membrana tympani, and the long process (A, 3, Fig. 11) is attached to the Glasserian fissure of the temporal bone. The malleus is articulated with the incus. The incus (B, Fig. 11) is connected with the posterior wall of the tympanic cavity, near the openings of the mastoid cells. It is articulated

FIG. 12.

The right temporal bone, the petrosal portion removed, showing the ossicles seen from within. —4, the incus, the short process of which is directed nearly in an horizontal direction backward; 5, the long process of the incus, free in the tympanic cavity, articulated with the stapes; 6, the malleus, articulated with the incus; 7, the long process of the malleus in the Glasserian fissure; 8, the stapes, articulated with the incus. This is drawn somewhat outward, otherwise, the base of the stapes alone would be visible. (RÜDINGER, *Atlas des Gehörganes*, München, 1867, Lieferung ii., Tafel ii.) This figure shows the handle of the malleus attached to the membrana tympani.

[1] In addition to the three bones ordinarily enumerated, Sappey, in the last edition of his work on anatomy, describes a very small bone, the lenticular bone, situated between the malleus and the stapes; but this is usually consolidated with the malleus, though it is sometimes united with the stapes, and is sometimes distinct. (SAPPEY, *Traité d'anatomie*, Paris, 1871, tome iii., p. 811.)

with the malleus, and, by the extremity of its long process (B, 2, Fig. 11), with the stapes. The stapes (C, Fig. 11) is the most internal bone of the middle ear. It is articulated by its smaller extremity with the long process of the incus. Its base is oval (C*, Fig. 11) and, with its annular ligament, is applied to the fenestra ovalis. The direction of the stapes is nearly at a right angle with the long process of the incus in the natural state (8, Fig. 12).

There are three well-defined muscles connected with the middle ear. Of these, two are attached to the malleus, and one, to the stapes.

The largest of the three muscles is the tensor tympani, called sometimes the internal muscle of the malleus. Its fibres arise from the cartilaginous portion of the Eustachian tube, the spinous process of the sphenoid bone, and the adjacent portion of the temporal. From this origin, it passes backward, almost horizontally, to the tympanic cavity. In front of the fenestra ovalis, it turns, nearly at a right angle, over a bony process, and its tendon is inserted into the handle of the malleus at its inner surface near the root. The tendon is very delicate, and the muscular portion is about half an inch in length (10, Fig. 10). The muscle and its tendon are enclosed in a distinct fibrous sheath. The action of this muscle is to draw the handle of the malleus inward, pressing the base of the stapes against the membrane of the fenestra ovalis, and producing tension of the membrana tympani. The fibres of this, and of all the muscles of the ear, are of the striated variety. The tensor tympani is supplied with motor filaments from the otic ganglion, which are probably derived from the facial nerve.[1]

The laxator tympani, the external muscle of the malleus, arises from the spinous process of the sphenoid bone and, by a few filaments, from the cartilaginous portion of the Eustachian tube. It passes backward, through the Glasserian fissure, to be inserted into the neck of the malleus, being en-

[1] See vol. iv., Nervous System, p. 420.

closed, in its course, in a fibrous sheath. The laxator tympani is generally believed to be muscular, though some authorities deny that it is composed of true muscular fibres. Its action would be to draw the malleus forward and outward, producing relaxation of the membrana tympani. It is not definitely known from what nerve this muscle derives its motor filaments.

The stapedius muscle is situated in the descending portion of the aqueductus Fallopii and in the cavity of the pyramid on the posterior wall of the tympanic cavity. Its tendon emerges from a foramen at the summit of the pyramid. In the canal in which this muscle is lodged, its direction is upward and vertical. At the summit of the pyramid, it turns at nearly a right angle, its tendon passing horizontally forward to be attached to the head of the stapes. Like the other muscles of the ear, this is enveloped in a fibrous sheath. Its action is to draw the head of the stapes backward, relaxing the membrana tympani. This muscle receives filaments from the facial nerve by a distinct branch, the tympanic.[1]

The posterior wall of the tympanic cavity presents several foramina which open directly into numerous irregularly-shaped cavities, communicating freely with each other, in the mastoid process of the temporal bone. These are called the mastoid cells. They are lined by a continuation of the mucous membrane of the tympanum. There is, under certain conditions, a free circulation of air between the pharynx and the cavity of the tympanum through the Eustachian tube, and from the tympanum to the mastoid cells.

The Eustachian tube (12, Fig. 10)[2] is partly bony and partly cartilaginous. Following its direction from the tympanic cavity, it passes forward, inward, and slightly downward. Its entire length is about an inch and a half. Its caliber gradually contracts from the tympanum to the spine

[1] See vol. iv., Nervous System, p. 149.

[2] EUSTACHIUS, *Epistola de Auditus Organis.—Opuscula Anatomica*, Venetiis, 1564, p. 148, *et seq.*

of the sphenoid, and from this constricted portion it gradually dilates to its opening into the pharynx, the entire canal presenting the appearance of two cones. The osseous portion extends from the tympanum to the spine of the sphenoid. The cartilaginous portion is an irregularly-triangular cartilage, bent upon itself above, forming a furrow, with its concavity presenting downward and outward. The fibrous portion occupies about half of the tube beyond the osseous portion, and completes the canal, forming its inferior and external portion. In its structure, the cartilage of the Eustachian tube is intermediate between the hyaline and the fibro-cartilage.

The circumflexus, or tensor-palati muscle, which has already been described in connection with deglutition,[1] is attached to the anterior margin, or hook of the cartilage. The attachments of this muscle have lately been accurately described by Rüdinger, who calls it the dilator of the tube,[2] though its action had been indicated by Valsalva, in the early part of the last century,[3] and was very fully described by Toynbee, in 1853.[4] The following excellent summary of the action of the muscles upon the tube is taken from the report on otology, by Dr. J. Orne Green, contained in the Transactions of the American Otological Society:[5]

"The relations and attachments of the muscles of the Eustachian tube have been recently demonstrated very satisfactorily by Rüdinger. The tensor-palati muscle is a dilator of the tube; it is inserted along the whole length of the hook

[1] See vol. ii., Digestion, p. 185.

[2] RÜDINGER, in STRICKER, *Manual of Human and Comparative Histology*, The New Sydenham Society, London, 1873, vol. iii., p. 71.

[3] VALSALVA, *De Aure Humana Tractatus.—Opera*, Lugd. Batav., 1742, p. 34. As some authors state that Valsalva did not describe the action of the dilator muscle, we quote the following: "* * * *nam si musculus iste leviter digitis trahatur, tunc nasi interna foramina, tubaque Eustachiana dilatantur.*"

[4] TOYNBEE, *Diseases of the Ear*, Philadelphia, 1860, p. 215. The original observations of Toynbee were presented to the Royal Society, in 1853.

[5] GREEN, *Report on the Progress of Otology, for* 1869–'70.—*Transactions of the American Otological Society*, Third Annual Meeting, New York, 1870, p. 9.

of the cartilage, passing forward, inward, and slightly downward, and its fibres spread out along the edge of the soft palate and on the side of the pharynx. In contracting, it draws the hook of the cartilage forward and a little downward, thus enlarging the calibre of the tube. The levator palati takes its origin from the temporal bone just below the osseous tube, and passes along the floor of the tube, some of its fibres arising from the lower end of the cartilage; it is inserted in the uvula, and, in contracting the belly of the muscle which lies along the floor of the tube, becomes thicker: the floor of the tube is raised, and the fibres arising from the cartilage serve to draw the lower end of this away from the opposite wall.

"The palato-pharyngeus rises from the posterior part of the lower end of the cartilage, passes backward, and is inserted on the posterior wall of the pharynx. Its action would be to draw the posterior wall of the tube backward; but, as it is often but slightly developed, it probably only serves to fix the cartilage, so that the other muscles can act more effectively.

"The opening of the tube is thus the result of the action of these three muscles: the tensor-palati, or dilator tubæ, draws the hook of the cartilage outward, the cartilage becomes less curved and the tube is widened; the levator palati in contracting becomes more horizontal, and draws the lower end of the cartilage inward and upward, thus enlarging the pharyngeal orifice more than 3‴. As soon as these muscles cease acting, the elasticity of the cartilage restores the canal to its former condition."

It is thus that the action of certain of the muscles of deglutition dilates the pharyngeal end of the Eustachian tube. If we close the mouth and nostrils, and make several repeated acts of deglutition, we draw the air from the tympanic cavity, and the atmospheric pressure renders the membrane of the tympanum tense, increasing its concavity. By one or two lateral movements of the jaws, we open the tube, the

pressure of air is equalized, and the ear returns to its normal condition. The above is the experiment indicated by Toynbee, as a demonstration of the action of the pharyngeal muscles;[1] but this observer was in error in supposing that the Eustachian tube is perfectly closed in the quiescent state; for there probably always remains a narrow chink admitting the passage of a small quantity of air; at least, this is the opinion of most modern writers upon the physiology of the ear, particularly Lucae and Schwartze, who noted an outward movement of the membrana tympani with the inspiratory act, in healthy persons during tranquil respiration.[2] In describing the dilator tubæ, Rüdinger states that he has confirmed the observations of Tröltsch and Mayer, who have shown that there is a direct transition of this muscle into the tensor tympani.[3] The nerves animating the dilator tubæ come from the pneumogastric and are derived from the spinal accessory.[4]

A smooth mucous membrane forms a continuous lining for the Eustachian tube, the cavity of the tympanum, and the mastoid cells. In all parts, it is closely adherent to the subjacent tissues, and, in the cavity of the tympanum, is very thin. In the cartilaginous portion of the Eustachian tube, there are numerous mucous glands, which are most abundant near the pharyngeal orifice, and gradually diminish in number toward the osseous portion, in which there are no glands. Throughout the tube, the surface of the mucous membrane is covered with conoidal cells of ciliated epithelium. The membrane of the tympanic cavity is very thin, consisting of little more than epithelium and a layer of connective tissue. It lines the walls of the cavity, the inner surface of the membrana tympani, is prolonged into the mastoid cells, and cov-

[1] TOYNBEE, *Diseases of the Ear*, Philadelphia, 1860.

[2] LUCAE, *Ueber die Respirationbewegung des Trommelfells.—Archiv für Ohrenheilkunde*, Würtzburg, 1864, Bd. i., S. 96, *et seq.*

SCHWARTZE, *Respiratorische Bewegung des Trommelfells.*—Ibid., S. 139, *et seq.*

[3] RÜDINGER, in STRICKER, *Manual of Human and Comparative Histology*, The New Sydenham Society, London, 1873, vol. iii., p. 71.

[4] See vol. iv., Nervous System, p. 207.

ers the ossicles and those portions of the muscles and tendons which pass through the tympanum. On the floor and on the anterior, inner, and posterior walls, the epithelium is of the conoidal, ciliated variety. On the promontory, roof, ossicles, and muscles, the cells are of the pavement variety and not ciliated, the transition from one form to the other being gradual. The entire membrane contains numerous lymphatics, a plexus of nerve-fibres and nerve-cells, with some peculiar cells, the physiology of which is not understood. The presence of mucous glands in the tympanic cavity, indicated by Tröltsch[1] and others, has been denied by Kessel, for the human subject, though he has found them in the cat and dog.[2]

We have thus given a general sketch of the physiological anatomy of the middle ear, and shall not find it necessary to treat more fully of the cavity of the tympanum, the mastoid cells, or the Eustachian tube, except as regards certain points in their physiology. The minute anatomy of the membrana tympani and the articulations of the ossicles can be more conveniently considered in connection with the physiology of these parts.

General Arrangement of the Bony Labyrinth.—The internal portion of the auditory apparatus is contained in the petrous portion of the temporal bone. It consists of an irregular cavity, called the vestibule, the three semicircular canals (13, 14, 15, Fig. 10), and the cochlea (16, Fig. 10). The general arrangement of these parts *in situ* and their relations to the adjacent structures are shown in Fig. 10. Fig. 13, showing the bony labyrinth isolated, is taken from the beautiful photograph contained in Rüdinger's atlas.

The vestibule is the central chamber of the labyrinth,

[1] TRÖLTSCH, *Diseases of the Ear*, New York, 1869, p. 174; and, *Anatomie de l'oreille*, Bruxelles, 1868, p. 94.

[2] KESSEL, in STRICKER, *Manual of Human and Comparative Histology*, The New Sydenham Society, London, 1873, vol. iii., p. 58.

communicating with the tympanic cavity by the fenestra ovalis, which is closed in the natural state by the base of the stapes. This is the central ovoid opening shown in Fig. 13. The inner wall of the vestibule presents a small, round de-

FIG. 13.

The left bony labyrinth of a new-born child, forward and outward view.—1, the wide canal, the beginning of the spiral canal of the cochlea; 2, the fenestra rotunda; 3, the second turn of the cochlea; 4, the final half-turn of the cochlea; 5, the border of the bony wall of the vestibule, situated between the cochlea and the semicircular canals; 6, the superior, or sagittal semicircular canal: 7, the portion of the superior semicircular canal bent outward; 8, the posterior, or transverse semicircular canal; 9, the portion of the posterior connected with the superior semicircular canal; 10, point of junction of the superior and the posterior semicircular canal; 11, the ampulla ossea externa; 12, the horizontal or external semicircular canal. (RÜDINGER, *Atlas des menschlichen Gehörorganes*, München, 1867, Lieferung i., Tafel v.) The explanation of this Figure has been modified and condensed from Rüdinger.

pression, the fovea hemispherica, perforated by numerous small foramina, through which pass nervous filaments from the internal auditory meatus. Behind this depression, is the opening of the aqueduct of the vestibule. In the posterior wall of the vestibule, are five small, round openings leading to the semicircular canals, with a larger opening below, leading to the cochlea.

The general arrangement of the semicircular canals is shown in Fig. 13 (6, 7, 8, 9, 10, 11, 12).

The arrangement of the cochlea, the anterior division of the labyrinth, is shown in Fig. 13 (1, 3, 4). This is a spiral canal, about an inch and a half long, and one-tenth of an inch wide at its commencement, gradually tapering to the apex, and making, in its course, two and a half turns. Its interior presents a central pillar, around which winds a spiral lamina of bone. The fenestra rotunda (2, Fig. 13), closed in the natural state by a membrane (the secondary membrana tympani), lies between the lower portion of the cochlea and the cavity of the tympanum.

What is called the membranous labyrinth is contained within the bony parts just described. Its structure, and the ultimate distribution and connections of the auditory nerve, which penetrates by the internal auditory meatus, involve some of the most intricate and difficult points in the whole range of minute anatomy. Some of these have direct and important relations to the physiology of hearing, while many are of purely anatomical interest. Such facts as bear directly upon physiology will be considered fully in connection with the functions of the internal ear.

CHAPTER VIII.

PHYSICS OF SOUND.

Laws of sonorous vibrations—Reflection and refraction of sound—Noise and musical sounds—Intensity, pitch, and quality of musical sounds—Mechanism of the siren—Musical scale—Harmonics, or overtones—Resonators of Helmholtz—Resultant tones—Summation tones—Harmony—Discord—Beats a cause of discord—Tones by influence (consonance).

THE sketch that we have given of the general anatomical arrangement of the auditory apparatus conveys an idea of the uses of the different parts of the ear. The waves of sound must be transmitted to the terminal extremities of the auditory nerve in the labyrinth. These waves are collected by the pinna, are conducted to the membrana tympani through the external auditory meatus, produce vibrations of the membrana tympani, are conducted by the chain of ossicles to the openings in the labyrinth, and are communicated through the fluids of the labyrinth to the ultimate nervous filaments. The free passage of air through the external meatus and the communications of the cavity of the tympanum with the mastoid cells, and, by the Eustachian tube, with the pharynx, are necessary to the proper vibration of the membrana tympani; the integrity of the ossicles and of their ligaments and muscles is essential to the proper conduction of sound to the labyrinth; the presence of liquid in the labyrinth is a condition essential to the conduction of the waves to the filaments of distribution of the auditory nerves; and, finally, from the labyrinth, the nerves pass through the internal auditory meatus to the brain, where the auditory impressions are appreciated.

Most of the points in acoustics which are essential to the comprehension of the physiology of audition are definitely settled. The theories of the propagation of sound involve wave-action, concerning which there is no dispute among physicists. For the conduction of sound, a ponderable medium is essential; and it is not necessary, as in the case of the undulatory theory of light, to assume the existence of an imponderable ether. The human ear, though perhaps not so acute as the auditory apparatus of some of the inferior animals, not only appreciates irregular waves, such as produce noise as distinguished from sounds called musical, but is capable of distinguishing regular waves, as in simple musical sounds, and harmonious combinations.

In music, certain successions of regular sounds are agreeable to the ear and constitute what we call melody. Again, we are able to appreciate, not only the intensity of sounds, both noisy and musical, but we recognize different qualities, particularly in musical tones. Still farther, we find that tones may be resolved into certain invariable component parts, such as the octave, the third, fifth, etc. These components of what are usually called simple tones may be isolated, in carefully-conducted experiments, but there is always a tone heard which predominates over others, the pitch and quality of which are readily appreciated by a practised musical ear.

The quality of tones may be modified by the simultaneous production of other tones which correspond to certain of the components of the predominating note. For example, if we add to a single tone, the third, fifth, and octave, we produce a major chord, the sound of which is very different from that of a single note or of a note with its octave. If we diminish the third by a semitone, we have a different quality, which is peculiar to minor chords. In this way, we can form an immense variety of musical sounds upon a single instrument, as the piano. And still farther, by the harmonious combinations of different notes of different instru-

ments and different registers of the human voice, as in grand choral and orchestral compositions, shades of effect, almost innumerable, may be produced. The modification of tones in this way constitutes harmony; and an educated ear, not only experiences pleasure from these musical combinations, but can distinguish their different component parts.

A chord may convey to the ear the sensation of completeness in itself, or it may lead to a succession of tones before this sense of completeness is attained. Different chords of the same key may be made to follow each other, or we may, by transition-tones, pass to the chords of other keys. Each key has its fundamental note, and the transition from one key to another, in order to be agreeable to the ear, must be made in certain well-defined and invariable ways. These regular transitions constitute modulation. The ear becomes fatigued by long successions of tones, always in one key, and modulation is essential to the enjoyment of elaborate musical compositions; otherwise, the tones would not only become monotonous, but their correct appreciation would be impaired, as the appreciation of colors becomes less distinct after looking for a long time at an object presenting a single vivid tint.

The history of music dates far back into antiquity, first consisting of the melodious succession of tones, and later, of both melody and harmony. Until within a comparatively recent period, the only analysis of tones was that of Pythagoras, who analyzed the sound produced by vibrating strings. He divided a vibrating string into two unequal sections, one twice the length of the other. Upon sounding these two divisions simultaneously, he found the note of the shorter division to be the octave of the longer. He then divided the string, so that its parts had the relation of two to three, and found the notes separated by an interval of a fifth. "Thus, dividing his string at different points, Pythagoras found the so-called consonant intervals in music to correspond with certain lengths of his string; and he made the extremely im-

portant discovery, that the simpler the relation of the two parts into which the string was divided, the more perfect was the harmony of the two sounds."[1] These important facts were developed more than five hundred years before the Christian era.

Laws of Sonorous Vibrations.

As we have already remarked, sound is produced by vibrations in a ponderable medium. The sounds ordinarily heard are transmitted to the ear by means of vibrations of the atmosphere. A simple and very common illustration of this fact is afforded by the experiment of striking a bell carefully arranged *in vacuo*. Though the stroke and the vibration can readily be seen, there is no sound; and, if air be gradually introduced, the sound will become appreciable and progressively more intense as the surrounding medium is increased in density. This interesting experiment was made by Hawksbee, in 1705;[2] but, to secure perfect success, it is necessary to suspend the bell in the exhausted receiver by threads, so that the vibrations cannot be conducted to the solid parts of the apparatus.

If we produce a single sound, or shock, in a free atmosphere, we may suppose that the waves are transmitted equally in every direction; and this is accomplished in the following manner: An imaginary sphere of air receives an impulse, or shock, from the body which produces the sound. This shock is, in its turn, communicated to another spherical stratum of air; this, to a third, and so on. The elasticity of the air, however, produces a recoil of each imaginary sphere of air, and it is a portion of the last stratum which strikes the tympanum, throwing it into vibration. If but a single impulse be given to the air, we may suppose that all of the different

[1] TYNDALL, *Sound*, London, 1867, p. 288.

[2] HAWKSBEE, *An Experiment made at a Meeting of the Royal Society, touching the Diminution of Sound in Air rarefy'd.—Philosophical Transactions*, for the Years 1704 and 1705, London, 1706, vol. xxiv., p. 1904.

strata, after a single oscillation, return to their original quiescent condition. The first stratum receives the shock, and the last communicates the shock to the ear. The oscillations of sound, produced in this way, are to and fro in the direction of the line of conduction, and are said to be longitudinal. In the undulatory theory of light, the vibrations are supposed to be at right angles to the line of propagation, or transversal. A complete oscillation to and fro is called a sound-wave.

It is evident that vibrating bodies may be made to perform and impart to the atmosphere oscillations of greater or less amplitude. The intensity of the sound is in proportion to the amplitude of the vibrations. If we cause a tuning-fork to vibrate, the sound is at first loud, or intense; but the amplitude gradually diminishes, and the sound dies away until it is lost. In a vibrating body capable of producing a definite number of waves of sound in a second, it is evident that the greater the amplitude of the wave, the greater is the velocity of the particles thrown into vibration. It has been ascertained by experiment, that there is an invariable mathematical relation between the intensity of sound, the velocity of the conducting particles, and the amplitude of the waves; and this is expressed by the formula, that the intensity is proportional to the square of the amplitude. It is evident, also, that the intensity of sound is diminished by distance, as the amplitude of the waves and the velocity of the vibrating particles become weaker, the farther we are removed from the sonorous body. The sound, as the waves recede from the sonorous body, becomes distributed over an increased area. The propagation of sound has been reduced also to the formula, that the intensity diminishes in proportion to the square of the distance.

Sonorous vibrations are subject to many of the laws of reflection which we have studied in connection with light. Sound may be absorbed by soft and non-vibrating surfaces, as certain surfaces absorb the rays of light. It is in this way that we explain the deadening of sound in apartments fur-

nished with carpets, curtains, etc., and their reflection from smooth, hard surfaces. By carefully-arranged convex surfaces, the waves of sound may be readily collected to a focus. These laws of the reflection of sonorous waves explain echoes and the conduction of sound by confined strata of air, as in tubes. We thus explain the mechanism of speaking-trumpets, the collection of the waves by the pavilion of the ear, and their transmission to the tympanum by the external auditory meatus. To make the parallel between sonorous and luminous transmission more complete, it has been ascertained that the waves of sound may be refracted to a focus by being made to pass through an acoustic lens, as a balloon filled with carbonic-acid gas. The waves of sound may also be deflected around solid bodies, when they produce what have been called by Tyndall, shadows of sound.[1]

Any one observing the sound produced by the blow of an axe can note the important fact that sound is transmitted with much less rapidity than light. At a short distance, our view of the body is practically instantaneous; but there is a considerable interval between the blow and the sound. This interval represents the velocity of the sonorous conduction. This fact is also illustrated by the interval between a flash of lightning and the sound of thunder. The velocity of sound depends upon the density and elasticity of the conducting medium. Without discussing the formulæ of Newton and their correction by Laplace, it is sufficient to state that the rate of conduction of sound by atmospheric air at the freezing-point of water is about 1,090 feet per second. This rate presents comparatively slight variations for the different gases, but is very much more rapid in liquids and in solids. In ordinary water, it is 4,708 feet per second; in iron or steel wire, about 16,000 feet, and in most woods, in the direction of the fibre, about the same.[2]

Noise and Musical Sounds.—There is a well-defined

[1] TYNDALL, *Sound*, London, 1867, p. 22. [2] TYNDALL, *op. cit.*, p. 26, *et seq.*

physical, as well as an æsthetic distinction between noise and music. Taking, as examples, single sounds, a sound becomes noise when the air is thrown into confused and irregular vibrations. A noise may be composed of a few musical sounds, when these are not in accord with each other, and sounds called musical are not always entirely free from discordant vibrations, as we shall see in studying musical sounds, properly so called. A noise possesses intensity, varying with the amplitude of the vibrations, and it may have different qualities, depending upon the form of its vibrations. We may call a noise dull, sharp, ringing, metallic, hollow, etc., thus expressing qualities that are readily understood. In percussion of the chest, the resonance is called vesicular, tympanitic, etc., distinctions in quality that are quite important. A noise may also be called sharp or low in pitch, as the rapid or slow vibrations predominate, without answering the requirements of musical sounds. These explanations, with the definition that a noise is a sound that is not musical, will be better understood after we have described some of the characters of musical vibrations.

A pure and simple musical sound consists of vibrations following each other at regular intervals, provided that the succession of waves be not too slow or too rapid. When the vibrations are too slow, we have an appreciable succession of impulses, and the sound is not musical. When they are too rapid, we recognize that the sound is excessively sharp, but it is then painfully acute and has no pitch that can be accurately determined by the auditory apparatus. Such sounds may be occasionally employed in musical compositions, but, in themselves, they are not strictly musical.

In musical sounds, we recognize duration, intensity, pitch, and quality. The duration depends simply upon the length of time during which the vibrating body is thrown into action. The intensity depends, as we have already stated, upon the amplitude of the vibrations, and has no relation whatsoever to pitch. Pitch depends absolutely upon the

rapidity of the regular vibrations; and quality, upon the combinations of different notes in harmony, the character of the harmonics of fundamental tones, and the form of the vibrations.

Pitch of Musical Sounds.—In discussing the pitch of musical sounds, we shall leave out of the question, for the present, the harmonics, which exist in nearly all musical tones and affect their quality, and confine ourselves to the study of simple vibrations. Such tones are those of great organ-pipes, which are deficient in harmonics and in over tones, and are almost entirely pure.

Pitch depends upon the number of vibrations. A musical sound may be of greater or less intensity; it may at first be quite loud and gradually die away; but the number of vibrations in a definite tone is invariable, be it weak or powerful. The rapidity of the conduction of sound does not vary with its intensity or pitch, and, in the harmonious combination of the sounds of different instruments, be they high or low in pitch, intense or feeble, it is always the same in the same conducting medium. Distinct musical tones may present an immense variety of qualities, but all tones of the same pitch have absolutely equal rates of vibration. Tones equal in pitch are said to be in unison. This fact, though simple, has a most important physiological bearing. In the first place, an educated ear can, without difficulty, distinguish slight differences in pitch, in ordinary musical tones.[1] Again, we ascertain by experiment that this power of appreciation of tones is restricted within well-defined limits, which vary slightly in different individuals. Without citing all of the numerous observations upon this point, we may state that Helmholtz, whose authority is the very highest, gives, as the

[1] Helmholtz states, on the authority of E. H. Weber, that "experienced musicians can appreciate a difference in pitch corresponding to a relation of vibrations of 1,000 to 1,001. This would equal about $\frac{1}{64}$ of a semitone." (HELMHOLTZ, *Théorie physiologique de la musique*, Paris, 1868, p. 183.)

range of sounds that can be legitimately employed in music, those of from 40 to 4,000 vibrations in a second, embracing about seven octaves. In an orchestra, the double bass gives the lowest note, which has 40·25 vibrations in a second, and the highest note, given by the small flute, has 4,752 vibrations. In grand organs, there is a pipe which gives a note of 16·5 vibrations, and the deepest note of modern pianos has 27·5 vibrations; but delicate shades of pitch in these low tones are not appreciable to most persons.[1] Sounds above the limits just indicated are painfully sharp, and their pitch cannot be exactly appreciated by the ear. The physiological interest connected with these facts is, that the limits of the appreciation of musical sounds are probably due to the anatomical arrangement of the auditory apparatus, as we have a limit to the acuteness of vision, which can be explained by the structure of the eye. This fact is the basis of the accepted theories of the appreciation of musical sounds.

The Siren.—As the ear is capable of distinguishing musical sounds in unison, if we can construct an apparatus by which we are able, not only to produce different tones, but to calculate accurately the number of vibrations of each, we can make an absolute demonstration of the facts just stated. Such an instrument is the siren, the tones of which can be compared by the ear with those produced by other instruments. It is not essential to our purpose to describe minutely the mechanism of the siren, as all that we desire is to understand, in general terms, the principle of its action.

The principle of the siren depends upon the fact that puffs of air, produced at regular intervals, will give rise to musical tones, the pitch of which is high in proportion to the rapidity of the puffs, each of which forms a sound-wave. In the siren, we have a fixed disk of metal, perforated with several series of orifices, which may be closed or opened at will. Of these, the outer series of openings presents usually sixteen

[1] HELMHOLTZ, *Théorie physiologique de la musique*, Paris, 1868, p. 24.

orifices, the next series, twelve, the next, ten, and the innermost series, eight. Above this fixed disk, is another disk, with corresponding openings, which can be made to rotate at a known rate. When the openings in the two disks are in exact apposition, the air passes freely, in a continuous current, from a tube connected with a chamber below the lower disk, out by a tube connected with the upper disk. If the perforations in the two disks be oblique, the direction of the inferior openings being opposite to those in the upper disk, a current of air through the apparatus will cause the upper disk to rotate, when the perforations will be closed and opened at regular intervals. It is not difficult to arrange a dial which will register the exact number of rotations of the upper disk in a given time. The rapidity of rotation depends upon the force of the current of air through the apparatus; and the tone is higher with the more powerful currents. Let us suppose, now, that we have the siren perfectly adjusted, with a bellows that will force an equable current of air through it, and a dial which records the exact number of turns of the rotating disk. We sound the note of a tuning-fork and blow air through the siren, regulating the current until the two notes are exactly in unison. When this is accomplished, we set the registering portion of the apparatus in action, and stop it at the end of precisely one minute. The conclusion of this illustrative experiment we quote from Tyndall: "I suddenly push *b* and stop the clock-work; and here recorded on the dials we have the exact number of revolutions performed by the disc. This number is 1,440. But the series of holes open during the experiment numbers 16; for every revolution, therefore, we had 16 puffs of air, or 16 waves of sound. Multiplying 1,440 by 16, we obtain 23,040 as the number of vibrations executed by the tuning-fork in a minute. Dividing this number by 60, we find the number of vibrations executed in a second to be 384.

"Having determined the rapidity of vibration, the length of the corresponding sonorous wave is found with the ut-

most facility. Imagine this tuning-fork vibrating in the free air. At the end of a second from the time it commenced its vibrations, the foremost wave would have reached a distance of 1,090 feet in air of the freezing temperature. In the air of this room, which has a temperature of about 15° C., it would reach a distance of 1,120 in a second. In this distance, therefore, are embraced 384 sonorous waves. Dividing, therefore, 1,120 by 384, we find the length of each wave to be nearly 3 feet."[1]

By the siren, the principle of which is simple and sufficiently easy of comprehension, we can measure, with mathematical accuracy, the number of vibrations executed by any body emitting a simple musical tone, and we thereby arrive at an absolute demonstration of the fact, that a tone in music is composed of equable waves of sound, and that, the higher the tone, the more rapid are the sonorous vibrations.

Musical Scale.—We have thus far considered simple musical tones, without any reference to the relations of different tones to each other. A knowledge of these relations lies at the foundation of the science of music; and, without a clear idea of certain of the fundamental laws of music, we cannot thoroughly comprehend the mechanism of audition.

It requires very little cultivation of the ear to enable us to comprehend the fact, that the successions and combinations of tones must obey certain fixed laws; and, long before these laws were the subject of mathematical demonstration, the relations of the different notes of the scale were established, merely because certain successions and combinations were agreeable to the ear, while others were discordant and apparently unnatural. Now that we are pretty thoroughly acquainted with the laws of vibrations, we can study the scale from a scientific, as well as an æsthetic point of view.

The most convenient tones for our study are those produced by vibrating strings, and the phenomena here ob-

[1] TYNDALL, *Sound*, London, 1867, p. 68.

served are essentially the same for all musical sounds; for it is by means of vibrations communicated to the air that the waves of sound find their way to the auditory apparatus. Let us take, to begin with, a string vibrating 24 times in a second. If this string be divided into two equal parts, each part will vibrate 48 times in a second. The note thus produced is the octave, or the 8th of the primary note, called the 8th, because the natural scale, as we shall see, contains eight notes, of which the first is the lowest and the last, the highest. We may divide the half again, producing a second octave, and so on, within the limits of our appreciation of musical tones. If we divide the string so that $\frac{2}{3}$ of its length will vibrate, we have 36 vibrations in a second, and this note is the 5th in the scale. If we divide the string again, so as to leave $\frac{4}{5}$ of its length, we have 30 vibrations, which gives the 3d note in the scale. These are the most natural subdivisions of the tone; and the 1st, 3d, 5th, and 8th, when sounded together, make what is known as the common major chord. Three-fourths of the length of the original string makes 32 vibrations, and gives the 4th note in the scale. If we take $\frac{8}{9}$ of the string, we have 27 vibrations, and the note is the 2d in the scale. With $\frac{3}{5}$ of the string, we have 40 vibrations in a second, or the 6th note in the scale. With $\frac{8}{15}$ of the string, we have 45 vibrations in a second, or the 7th note in the scale.

It will be observed that we have started with a note, which we call C. This is the key-note, or the tonic. In this scale, which is called the natural, or diatonic key, we have a regular mathematical progression from the 1st to the 8th. This is called the major key of C. Melody consists in an agreeable succession of tones, which we may assume, for sake of simplicity, to be pure. We cannot, in a simple melody, sound any note but one of those in the scale. When a different note is sounded, we pass into a key which has a different fundamental note, or tonic, with a different succession of 3ds, 5ths, etc. Every key, therefore, has its 1st, 3d, 5th,

and 8th, as well as the intermediate notes. If we diminish the 3d by half a tone, which is formed by a string $\frac{5}{6}$ the length of the tonic, instead of $\frac{4}{5}$, we have the key converted into the minor. The minor chord, consisting of the 1st, the diminished 3d, the 5th, and the 8th, is perfectly harmonious, but has a quality quite different from that of the major chord. The notes of a melody may progress in the minor key as well as in the major. Taking the small numbers of vibrations merely for convenience, the following is the mode of progression in the natural scale of C major:

	1st.	2d.	3d.	4th.	5th.	6th.	7th.	8th.
Note, . . .	C	D	E	F	G	A	B	C
Lengths of the string,	1	$\frac{8}{9}$	$\frac{4}{5}$	$\frac{3}{4}$	$\frac{2}{3}$	$\frac{3}{5}$	$\frac{8}{15}$	$\frac{1}{2}$
Number of vibrations,	24	27	30	32	36	40	45	48

The intervals between the notes of the scale, it is seen, are not equal. The smallest, between the 3d and 4th and the 7th and 8th, are called semitones. The other intervals are either full perfect tones or small perfect tones.[1] Although there are semitones, not belonging to the key of C, between C and D, D and E, F and G, G and A, and A and B, these intervals are not all composed of exactly the same number of vibrations; so that, taking the notes on a piano, if we have D as the tonic, its 5th would be A. We assume that D has 27 vibrations, and A, 40, giving a difference of 13. With C as the tonic and G as the 5th, we have a difference of 12. It is on account of these differences in the intervals, that each key in music has a peculiar and an individual character.

In tuning a piano, which is the single instrument most commonly used for accompaniment and the general interpretation of musical compositions, the ordinary method is by

[1] Although a tone and a semitone do not have an absolutely-fixed value, they are usually defined as above; but a maximum tone is the interval between the 4th and 5th, equal, in the scale we have given, to four vibrations. A minimum tone is the interval between the 3d and 4th, or the 7th and 8th, equal to two or three vibrations. (LAUGEL, *La voix, l'oreille et la musique*, Paris, 1867, p. 121, note.)

the 5ths. We bring the 5th of C in exact accord with the tonic; then the 5th of D; then the 5th of E, and finally the 5th of F. The 5th of F should be the octave of C, but, by progressing in this way, the last note, C, is too sharp, and is not the octave of the lower C. If this progression were continued higher and higher, the octaves would become more and more out of tune; and, to avoid this, the octaves are made perfect and the 5ths and 3ds are tuned down, so that the inequality is distributed throughout the scale. This is called tempering the scale, and, with this "temperament," the notes are not exactly true; still, musicians are accustomed to this, and fail to recognize the mathematical defect.[1]

Even in melody, and still more in harmony, in long compositions, the ear becomes fatigued by a single key, and it is necessary, in order to produce the most pleasing effects, to change the tonic, by what is called modulation, returning afterward to the original key.

Quality of Musical Sounds.—By appropriate means, we can analyze or decompose white light into prismatic colors; and, in the same way, nearly all musical tones, which seem at first to be simple, can be resolved into certain well-defined constituents. There are few absolutely simple sounds used in music. We may take an example, however, in the tones of great stopped-pipes in the organ. These are simple, but are of an unsatisfactory quality, and wanting in richness. Almost all other tones, however, have a fundamental note, which we recognize at once; but this note is accompanied by harmonics caused by secondary vibrations of subdivisions of the sonorous body.

The number, pitch, and intensity of these harmonic, or partial vibrations affect what is called the quality, or timbre of musical tones, by modifying the form of the sonorous

[1] Helmholtz, in the great work we have so often quoted, discusses the faults and inaccuracies of the temperament very fully. (*Théorie physiologique de la musique*, Paris, 1868, p. 411, *et seq.*)

waves. This fact, which we shall discuss more elaborately farther on, requires little argument for its support. If we suppose a string vibrating a certain number of times in a second, the vibrations being perfectly simple, we should have, according to the laws of vibrating bodies, a simple musical tone; but, if we suppose that the string subdivides into different segments, one of which gives the 3d, another, the 5th, and so on, of the fundamental note, it is evident that the form of the vibrations must be considerably modified. This is the fact; and, with these modifications in form, the quality, or timbre, of the tone is changed. We can illustrate this roughly on the piano. If we strike the note C, we have a certain quality of sound. We may assume, for sake of argument, that this is a simple tone, though in reality it is complex. We now strike simultaneously the fundamental note, its 3d, 5th, and 8th, making the common chord of C major. The predominant tone is still C, but the addition of the harmonious notes modifies its quality. If we diminish the third by half a tone, we still have C for the predominant tone, but the quality of the chord is changed to the minor. In this rough illustration, the ear can readily detect the harmonious tones; but, in the tone of a single string, this cannot be done without practice and close attention. Still, in the tones of single strings, the ear can distinguish the harmonics; and, what is more satisfactory, the existence of harmonics can be actually demonstrated in various ways.

From what we have just stated, it follows that nearly all musical tones consist, not only of a fundamental sound, but of harmonic vibrations, subordinate to the fundamental and qualifying it in a particular way. These harmonics may be feeble or intense; certain of them may predominate over others; some, that are usually present, may be eliminated; and, in short, they may present great diversity of arrangement, and thus the timbre may present an infinite variety. This is one of the elements entering into the composition of tones, and affords a partial explanation of quality.

Another element in the quality of tones depends upon their reënforcement by resonance. The vibrations of a stretched string, not connected with a resonant body, are almost inaudible.[1] In musical instruments, we have the tone taken up by some mechanical arrangement, as the sound-board of the organ, piano, violin, harp, guitar, etc. In the violin, for example, the sweetness of the tone depends chiefly upon the construction of the resonant part of the instrument, and but little upon the strings themselves, which are frequently changed. The same is true of the human voice, of wind-instruments, etc. We could not discuss these points elaborately, without giving a full description of the various musical instruments in common use, which would be out of place in a work on physiology.

In addition to the harmonic tones of sonorous bodies, various discordant sounds are generally present, which modify

[1] The reënforcement of sounds by resonance is beautifully illustrated by an experiment originally made by Wheatstone, which is very graphically described by Tyndall, in his lectures on sound. (TYNDALL, *Sound*, London, 1867, p. 80.)

"We are now prepared to appreciate an extremely beautiful experiment, for which we are indebted to Prof. Wheatstone, and which I am now able to make before you. In a room underneath this, and separated from it by two floors, is a piano. Through the two floors passes a tin tube 2½ inches in diameter, and along the axis of this tube passes a rod of deal, the end of which emerges from the floor in front of the lecture-table. The rod is clasped by India-rubber bands, which entirely close the tin tube. The lower end of the rod rests on the sound-board of the piano, its upper end being exposed before you. An artist is at this moment engaged at the instrument, but you hear no sound. I place this violin upon the end of the rod; the violin becomes instantly musical, not however with the vibrations of its own strings, but with those of the piano. I remove the violin, the sound ceases; I put in its place a guitar, and the music revives. For the violin and guitar I substitute this plain wooden tray; it is also rendered musical. Here, finally, is a harp, against the sound-board of which I cause the end of the deal rod to press; every note of the piano is reproduced before you. I lift the harp so as to break its connection with the piano, the sound vanishes; but the moment I cause the sound-board to press upon the rod, the music is restored. The sound of the piano so far resembles that of the harp that it is hard to resist the impression that the music you hear is that of the latter instrument. An uneducated person might well believe that witchcraft is concerned in the production of this music."

the timbre, producing, usually, a certain roughness, such as the grating of a violin-bow, the friction of the columns of air against the angles in wind-instruments, etc. All of these conditions have their effect upon the quality of tones; and these discordant sounds may exist in infinite number and variety. These sounds are composed of irregular vibrations, and are consequently inharmonious. Nearly all tones that we speak of in general terms as musical are composed of musical, or harmonic partial tones, and the discordant elements to which we just alluded.

Aside from the relations of the various component parts of musical tones, the quality depends largely on the form of the vibrations. To quote the words of Helmholtz, "the more uniformly rounded the form of the wave, the softer and milder is the quality of the tone. The more jerking and angular the wave-form, the more piercing the quality. Tuning-forks, with their rounded forms of wave, have an extraordinarily soft quality; and the qualities of tone generated by the zither and violin resemble in harshness the angularity of their wave-forms."[1]

Harmonics, or Overtones.—As we have stated in the foregoing paragraphs, nearly all tones are composite, but some contain many more partial, or secondary vibrations than others. The tones of vibrating strings are peculiarly rich in harmonics, and these may be used for illustration, remembering that the phenomena here observed have their analogies in nearly all varieties of musical sounds. If a stretched string be made to vibrate, the secondary tones, which qualify, as it were, the fundamental, are called harmonics, or, in German, overtones, a term which is now much used by English writers.

While it is difficult at all times to distinguish by the ear the individual overtones of vibrating strings, their existence can be demonstrated by a few simple experiments. Let us

[1] Helmholtz, *Popular Lectures on Scientific Subjects*, New York, 1873, p. 77.

suppose, for example, that we have a string, the fundamental note of which is C. We damp this string with a feather at one-fourth of its length and draw a violin-bow across the smaller section. We then sound, not only the fourth part of the string, across which the bow is drawn, but the remaining three-fourths; but if we have placed little riders of paper upon the longer segment, at distances equal to one-fourth of the entire string, they will remain undisturbed, while riders placed at any other portion of the string will be thrown off. This experiment shows that the three-fourths of the string have been divided, as we have sounded the second octave above the fundamental note. This may be illustrated by connecting one end of the string with a tuning-fork. When this is done, and the string is brought to the proper degree of tension, it will first vibrate as a whole, then, when a little tighter, will spontaneously divide into two equal parts, and, under increased tension, into three, four, and so on. By damping a string with the light touch of a feather, we suppress the fundamental note and bring out the overtones, which exist in all vibrating strings, but are usually concealed by the fundamental. The points which mark the subdivisions of the string into segments of secondary vibrations are called nodes. When we damp the string at its centre, we quench the fundamental note and have overtones an octave above; damping it at a distance of one-fourth, we have the second octave above, and so on. When we damp it at a distance of one-fifth from the end, we have the four-fifths sounding the 3d of the fundamental, with the second octave of the 3d. If we damp it at a distance of two-thirds, we have the 5th of the fundamental, with the octave of the 5th.

Every vibrating string possesses, thus, a fundamental tone and overtones. We have, qualifying the fundamental, first, as the most simple, a series of octaves; next, a series of 5ths of the fundamental and their octaves; and next, a series of 3ds. These are the most powerful overtones, and form the common chord of the fundamental; but they are so far concealed by

the greater intensity of the fundamental, that they cannot be easily distinguished by the unaided ear, unless the fundamental be quenched in some such way as we have indicated. In the same way, the harmonic 5ths and 3ds overpower other overtones; for we have the string subdividing again and again into overtones, which are not harmonious like the notes of the common chord of the fundamental.

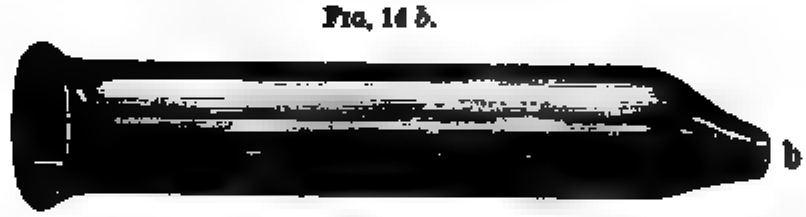
The presence of overtones, resultant tones, and additional tones, which latter will be described hereafter, can be demonstrated, without damping the strings, by the resonators, invented by Helmholtz. It is well known that, if a glass tube, closed at one end, which contains a column of air of a certain length, be brought near a resounding body sounding a note identical with that produced by the vibrations of the column of air, the air in the tube will resound in consonance with the note. If, for example, we have a tube sounding C, a tuning-fork of the same tone sounded near the tube will throw the air in the tube into action, and will produce a powerful sound, while no other note will have this effect. The resonators of Helmholtz are constructed on this principle. A glass globe or tube (Fig. 14) is constructed so as to produce a certain tone. This has a larger opening, a, and a smaller opening, b, which latter is fitted in the ear by warm sealing-wax, the other ear being closed. When the proper note is sounded, it is reënforced by the resonator and is greatly increased in intensity, while all other notes are heard very faintly. Suppose, now, that we apply this to the detection of overtones! We fix in the ear a resonator adjusted to G, and sound the fundamental, C. The fundamental, C, is imperfectly heard, but the overtone, G, is reënforced, and we have a loud and distinct sound of the 5th. By using resonators graduated to the musical scale, we can easily analyze a tone and distinguish the overtones. In the same way, if we fix in the ear a resonator tuned to a particular note and strike a succession of chords on the piano, the general sound is imperfectly heard; but, whenever we strike the note of the

resonator, this is clearly distinguished, to the practical exclusion of all others, and we can thus analyze complicated chords into each of their constituent parts. This experiment shows the similarity between chords, resolved into their constituent parts, and single tones, resolved into their harmonics,

Fig. 14 *a*.

a b

Fig. 14 *b*.

a  b

or overtones. The resonators of Helmholtz, which are open at the larger extremity, are infinitely more delicate than those in which this is closed by a membrane.[1]

A very beautiful and instructive point in the present discussion is the following: All the overtones are produced by vibrations of segments of the string included between the comparatively still points, called nodes; and, if we cause a string to vibrate by plucking or striking it at one of these nodal points, we abolish the overtones which vibrate from this node at a fixed point. For example, if we pluck the

[1] Helmholtz, *Théorie physiologique de la musique*, Paris, 1868, p. 57, *et seq.*, and p. 487.

string at its exact centre, we sound the fundamental, but have a dull tone, which is deficient in the overtones of the octaves. We can demonstrate the fact that these overtones are absent, for, if we damp the string at its centre, the fundamental is quenched, but we have no octaves, which are always heard on damping the centre when the string is plucked at other points. In the same way, by plucking the string at different points, we can abolish the overtones of 5ths, 3ds, etc. It is readily understood that, when a string is plucked at any point, it will vibrate so vigorously at this point that no node can be formed. This fact has long been recognized by practical musicians, though many are probably unacquainted with its scientific explanation. Performers on stringed instruments habitually attack the strings near their extremities. In the piano, where the strings may be struck at almost any point, the hammers are placed at from $\frac{1}{9}$ to $\frac{1}{7}$ of their extremities; and it has been ascertained by experience that this gives the richest tones. The nodes formed at these points would produce the 7ths and 9ths as overtones, which do not belong to the perfect major chord, while the nodes for the harmonious overtones are undisturbed.[1] The reason, then, why the tones are richer and more perfect, when the strings are attacked at this point, is that the harmonious overtones are full and perfect, and certain of the discordant overtones are suppressed.

The facility with which certain notes may be produced on the cornet affords another illustration of the natural subdivision of tones. In some parts of the scale, the open notes are the tonic, 8th, 5th, and 3d; that is, these notes can be produced by the lips and the currents of air, without altering the length of the column of air in the instrument by the valves. While some other of the notes in the scale may be produced by the action of the lips alone, they are formed in this way with uncertainty and difficulty. We can sound, for example, the minor 3d, the 4th, or the 6th, with the lips; but these tones are more exact when we use the valves, as is al-

[1] HELMHOLTZ, *Théorie physiologique de la musique*, Paris, 1868, p. 109.

most always done. But the notes of the common major chord, especially the 8th and 5th, are produced without using the valves; for the column of air in the instrument has a natural tendency to divide itself into its harmonic tones.

It was ascertained in the middle of the last century, by Sorge and by Tartini, that when two harmonious tones are produced under favorable circumstances, we can hear, in addition to the two sounds, a sound differing from both, and much lower than the lower of the two. This sound is too low for an harmonic, and has been called a resultant tone. The formation of a new sound by combining two sounds of different pitch is analogous to the blending of colors in optics, except that the primary sounds are not lost. The laws of the production of these resultant sounds are very simple. When two tones in harmony are sounded, the resultant tone is equal to the difference between the two primaries. For example, if we sound C, with 48 vibrations, and its 5th, with 72 vibrations in a second, the resultant tone is equal to the difference, which is 24 vibrations, and is consequently the octave below C; or, if we sound C, with 48 vibrations, and its 3d, with 60, we have a resultant tone two octaves below C, the number of vibrations being 12.[1] These resultant tones are very feeble as compared with the primary tones, and can only be heard under the most favorable experimental conditions. In addition to these sounds, Helmholtz has discovered sounds, even more feeble, which he calls additional, or summation tones.[2] The value of these is equal to the sum of vibrations of the primary tones. For example, C 24 and its 5th, 36, would give a summation tone of 60 vibrations, or the octave of the 3d; and C 24 with its 3d, 30, would give 54 vibrations, the octave of the 2d. These tones can readily be distinguished by means of the resonators already described.[3]

[1] These numbers are used merely in illustration. A sound of 12 vibrations does not come within the musical scale.

[2] HELMHOLTZ, *Théorie physiologique de la musique*, Paris, 1868, p. 192.

[3] See page 184.

It is thus seen that musical sounds are excessively complex. With single sounds, we have an infinite variety and number of harmonics, or overtones, and in chords, which will be treated of more fully under the head of harmony, we have a series of resultants, which are lower than the primary tones, and a series of additional, or summation tones, which are higher; but both the resultant and the summation tones bear an exact mathematical relation to the primary tones of the chord.

Harmony.—We have discussed the overtones, resultant tones, and summation tones of strings rather fully, for the reason that, in the physiology of audition, we shall see that the ear is capable of recognizing single sounds, or successions of single sounds; but, at the same time, certain combinations of sounds are appreciated, and are even more agreeable than those which are apparently produced by simple vibrations. Combinations of tones which thus produce an agreeable impression are called harmonious. They seem to become blended with each other into a complete sound of peculiar quality, all of the different vibrations entering into their composition being simultaneously appreciated by the ear. From what we have learned of overtones, it is evident that few musical sounds are really simple, and that those which are simple are wanting in richness, while they are perfectly pure. The blending of tones which bear to each other a certain mathematical relation is called harmony; but two or more tones, though each one be musical, are not necessarily harmonious. The most prominent overtone, except the octave, is the 5th, with its octaves, and this is called the dominant. The next is the 3d, with its octaves. The other overtones are comparatively feeble. Reasoning, now, from our knowledge of the relations of overtones, we might infer that the reënforcement of the 5th and 3d by other notes bearing similar relations to the tonic would be agreeable. This is the fact, and it was ascertained empirically long before the pleasing impression pro-

duced by such combinations was explained mathematically. We do not propose to enter into a full discussion of the laws of harmony, but a knowledge of certain of these laws is essential to the comprehension of the physiology of audition. These are very simple, now that we have analyzed the tone of a single vibrating body.

It is a law in music, that the more simple the ratio between the number of vibrations in two sounds, the more perfect is the harmony. The simplest relation, of course, is 1 : 1, when the two sounds are said to be in unison. The next in order is 1 : 2. If we sound C and its 8th, we have, for example, 24 vibrations of one to 48 of the other. These sounds can produce no discord, because the waves never interfere with each other, and the two sounds can be prolonged indefinitely, always maintaining the same relations. The combined impression is therefore continuous. The next in order is the 1st and 5th, their relations being 2 : 3. In other words, with the 1st and 5th, for two waves of the 1st, we have three waves of the 5th. The two sounds may thus progress indefinitely, for the waves coincide for every second wave of the 1st and every third wave of the 5th. The next in order, if we sound at the same time the 1st, 5th, and 8th, is the 3d. The 3d of C has the 8th of C for its 5th, and the 5th of C for its minor 3d. The 1st, 3d, 5th, and 8th form the common major chord; and the waves of each tone blend with each other at such short intervals of time that the ear experiences a continuous impression, and no discord is appreciated. This explanation of the common major chord illustrates the law that, the smaller the ratio of vibration between different tones, the more perfect is their harmony. Sounded with the 1st, the 4th is more harmonious than the 3d; but its want of harmony with the 5th excludes it from the common chord. The 1st, 4th, and 8th are harmonious, but to make a complete chord we must use the 6th. These discussions might be extended into the progression of chords and modulation; but this is not essential to our pur-

pose, as we wish only to ascertain the laws of the vibrations of sounds in harmony and the mechanism of discords.

Discords.—A knowledge of the mechanism of simple accords enables us to understand more easily the rationale of discords, and *vice versa.* As in the case of harmony, the fact that certain combinations of musical tones produce a disagreeable impression was ascertained empirically, with no knowledge of the exact cause of the palpable dissonance. Thanks to the labors of modern physicists, however, the mechanism of discords is now pretty well settled. We shall, in our explanation, begin with a combination of tones slightly removed from perfect unison.

Suppose, for example, that we have two tuning-forks giving precisely the same numbers of vibrations in a second; the tones are then in perfect unison. We load one of the forks with a bit of wax, so that its vibrations are slightly reduced, and start them both in vibration at the same instant. Taking the illustration given by Tyndall, we assume that one fork has 256, and the other, 255 vibrations in a second. While these two forks are vibrating, we have one gradually gaining upon the other; but, at the end of half a second, one will have made 128 vibrations, while the other will have made 127½. At this point the two waves are in direct opposition to each other; they are moving in exactly opposite directions; and, as a consequence, the sounds neutralize each other, and we have an instant of silence.[1] The perfect sounds,

[1] It is almost essential to this point in our argument to ascertain if two sounds in unison, so arranged that the maximum of the waves of one will coincide with the minimum of the waves of the other, will, when thus combined, produce silence. This fact has been illustrated by an example, which we quote from Helmholtz:

"Suppose that we have two organ-pipes, precisely similar, tuned in unison, placed near each other upon the same sound-board. Each one, sounded simply by a current of air, gives an intense tone; but if the current of air strike them both simultaneously, the movement of the air is modified in such a manner, that the current enters one of the pipes when it emerges from the other; no sound strikes the ear of an observer at a little distance, who then can only hear the

as the two forks continue to vibrate, are thus alternately re-enforced and diminished, and we have what are known in music as beats. As the difference in the number of vibrations in a second is one, we have the instants of silence occurring once in a second; and, in this illustration, the beats occur once a second. Unison takes place when two sounds can follow each other indefinitely, their waves blending perfectly; dissonance is marked by successive beats, or pulses. If we now load forks so that one will vibrate 240 times in a second, and the other 234, there will be six times in a second when the interference will be manifest; or, to make it plainer, in $\frac{1}{6}$ of a second, one fork will make 40 vibrations, while the other is making 39. We shall then have 6 beats in a second. From these experiments, the law may be deduced, that the number of beats produced by two tones not in harmony is equal to the difference between the two rates of vibration.[1] An analogous interference of undulations is observed in optics, when waves of light are made to interfere and produce darkness.

It is evident that the number of beats will increase as we sound two discordant tones higher and higher in the scale. According to Helmholtz, the beats can be recognized up to 132 in a second. Beyond that point, they become confused, and we have only a sensation of dissonance, or roughness.[2] We can illustrate this point very satisfactorily by a simple experiment upon the piano. Let us take two tones, the highest on the scale, separated from each other by a semitone. When we strike these two notes together, we have a disagreeable sensation of dissonance, but no appreciable beats, because, the rate of vibration of each note being high, the difference is great and the beats are too rapid to be appreciated as such. We strike, now, the two notes an octave be-

rushing of the air." (HELMHOLTZ, *Théorie physiologique de la musique*, Paris, 1868, p. 201.)

[1] TYNDALL, *Sound*, London, 1867, p. 268.

[2] HELMHOLTZ, *op. cit.*, p. 217.

low; still we have dissonance, less disagreeable, but no beats. Passing down, an octave at a time, as the numbers of vibrations become smaller, the difference between them is less, and there are fewer beats in a second, until they are readily appreciated as beats and can even be counted.

Beats, then, are due to interference of sound-waves, and the number in a second is equal to the difference in the rate of vibrations. When these are too rapid to be appreciated as beats, we have simply a sensation of discord. There is no interference of the waves of tones in unison, provided the waves start at the same instant; the intensity of the sound being increased by reënforcement. The differences between the 1st and 8th, the 1st and 5th, the 1st and 3d, and other harmonious combinations, is so great that we have no beats and no discord, the more rapid waves reënforcing the harmonics of the primary sound. It is important to remember, in this connection, that resultant tones are equal to the difference in the rates of vibration of two harmonious tones. If we take a note of 240 vibrations, and its 5th, with 360 vibrations, these two have a difference of 120, which is the lower octave of the 1st and is an harmonious tone.

It is evident that the laws which we have thus stated are equally applicable to overtones, resultant tones, and additional tones, which have their beats and dissonances, as well as the primary tones.

Tones by Influence (*Consonance*).—The term consonance is generally applied to the harmonious combinations of two or more sounds, and is synonymous with accord, as it is used in music. In this sense, it is opposed to dissonance, or discord. By some writers, however, consonance is used to denote sounds produced in sonorous bodies by the influence of sounds in unison. If, for example, we have a bell tuned to a certain note, and bring near its opening a tuning-fork vibrating in unison with this note, the bell will sound vigorously in unison, though it is influenced only by the vibra-

tions in the air produced by the primary tone. We have already spoken of this under the head of resonance;[1] and sounds produced in this way are properly called tones by influence.

It is evident that the mechanism of the production of tones by influence cannot be neglected in studying the physiology of audition. We have, as an important part of the auditory apparatus, the membrane of the tympanum, capable of various degrees of tension, which is thrown into vibration in obedience to waves of sound conducted by the atmosphere; and it will be an important point to determine how far the vibrations of this membrane are affected by the laws of the production of tones by influence.

After what we have learned of the laws of musical vibrations, it will be easy to comprehend the production of tones by influence. We shall take first the most simple example, applied to strings. If we gently touch the note C upon the piano, so as to raise the damper but not sound the string, and then sing a note in unison, the string will return the sound, by the influence of the sound-waves. The sound thus produced by the string will have its fundamental tone and overtones; but the series of overtones will be complete; for none of the nodes are abolished, as in striking or plucking the string at any particular point. If, instead of the note in unison, we sing any of the octaves, the string will return the note sung; and the same is true of the 3d, 5th, etc. If we now strike a chord in harmony with the undamped string, this chord will be exactly returned by influence. In other words, a string may be made to sound by influence, its fundamental note, its harmonics, and harmonious combinations. To carry the observation still farther, the string will return, not only a note of its exact pitch and its harmonics, but notes of the quality of the primary tone. This is a very important point in its applications to the physiology of hearing, and can be readily illustrated. Taking identical tones in suc-

[1] See page 184.

cession, produced by the voice, trumpet, violin, clarinet, or other musical instruments, it can be easily noted that the quality of the tone, as well as the pitch, is rendered by a resounding string; and the same is true of combinations of tones.

The above laws of tones by influence have been illustrated by strings merely for the sake of simplicity; but they have a more or less perfect application to all bodies capable of producing musical tones, except that some are thrown into vibration with more difficulty than others. An interesting application of these laws, however, particularly with reference to the physiology of the ear, is in the case of stretched membranes; for this brings to our mind the possible action of the membrana tympani.

If we have a thin membrane, like a piece of bladder or thin rubber, stretched over a circular orifice, such as the mouth of a wide bottle, this can be tuned to a certain note. When arranged in this way, the membrane can be made to sound its fundamental note by influence. In addition, the membrane, like a string, will divide itself so as to sound the harmonics of the fundamental, and will likewise be thrown into vibration by the 5th, 3d, etc., of its fundamental tone, thus obeying the laws of vibrations of strings, though the harmonic sounds are produced with greater difficulty.

At about the beginning of this century, Chladni demonstrated the spontaneous division of vibrating plates and membranes by a very simple experiment.[1] He covered the surface with a delicate, uniform layer of fine sand. Arranged in this way, it is evident that the sand would be thrown off from the vibrating portions and collected upon those portions which remained comparatively quiescent, provided that the surface became divided into different areas of vibration. This was ascertained to be the fact. When the fundamental tone was sounded, the entire plate was thrown into vibration, and the sand was collected in a circular line near its periphery; and,

[1] CHLADNI, *Die Akustik*, Leipzig, 1802, S. xvi., 78, *et seq.*, and S. 118, *et seq.*

with each harmonic, a smaller circle was produced. These marked the nodal lines, which correspond to the harmonic nodes of vibrating strings. Chladni applied these observations to the vibrations of round and square plates of glass fixed at the centre, damped by the finger at various points, and thrown into vibration by a violin-bow. In 1824, Savart repeated many of the experiments of Chladni, and extended them to the membrana tympani of the human subject, in which he observed analogous phenomena, though they were less distinct, on account of the small extent of the vibrating surface.[1] Of course, the vibrations of the membrana tympani must take place in accordance with physical laws; but how far these laws are applicable to the physiology of audition, is a question which we shall discuss fully in connection with the functions of different portions of the auditory apparatus.

We have thus discussed various points in the physics of sound, some of them with an elaborateness which might seem out of place in a work on physiology. It must be remembered, however, that the laws of acoustics are nearly all definitely settled; that we have an absolutely-certain mathematical demonstration of the laws of musical vibrations; and that the ear recognizes these laws, and recognized them long before they were ascertained by physical experimentation, for certain sounds and combinations of sound simply give pleasure, while others are disagreeable and discordant. It is sufficiently evident that, if musical combinations be subjected to certain inevitable laws, these laws form the only true basis of the study of the mechanism of audition. It will be found, indeed, that no point has been discussed in this chapter, that is not essential to a clear comprehension of the physiology of hearing.

[1] SAVART, *Recherches sur les usages de la membrane du tympan et de l'oreille externe.—Journal de physiologie*, Paris, 1824, tome iv., p. 188, *et seq.*

CHAPTER IX.

USES OF DIFFERENT PARTS OF THE AUDITORY APPARATUS.

Uses of the external ear—Structure of the membrana tympani—Uses of the membrana tympani—Variations in tension—Vibrations of the membrane by influence—Destruction of the membrana tympani—Appreciation of the pitch of tones—Mechanism of the ossicles of the ear—Articulations and attachments of the ossicles—Physiological anatomy of the internal ear—General arrangement of the membranous labyrinth—Vestibule—Semicircular canals—Cochlea—Liquids of the labyrinth—Distribution of nerves in the cochlea—Organ of Corti—Functions of different parts of the internal ear—Functions of the semicircular canals—Functions of the parts contained in the cochlea—Summary of the mechanism of audition.

THE uses of the pavilion of the ear and of the external auditory meatus are sufficiently apparent. The pavilion serves to collect the waves of sound, and probably inclines them toward the external meatus as they come from various directions. Though this action is simple, it undoubtedly has a certain degree of importance, and the various curves of the concavity of the pavilion tend more or less to concentrate the sonorous vibrations. Such has long been the opinion of physiologists, and this seems to be carried out by experiments in which the concavities of the external ear have been obliterated by wax.[1] There is, probably, no resonance or vibration of much importance until the waves of sound strike the membrana tympani. The same remarks may be made with regard to the external auditory meatus. We do not know precisely how the obliquity and the curves of this canal affect the waves of sound, but we may suppose that the deviation from a straight course protects, to a certain degree,

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 14.

the tympanic membrane from impressions that might otherwise be too violent.

Structure of the Membrana Tympani.—The general arrangement of the membrana tympani has already been described in connection with the topographical anatomy of the auditory apparatus.[1] This structure, which is of great importance in the physiology of hearing, is delicate, elastic, about the thickness of ordinary gold-beater's skin, and is subject to various degrees of tension, from the action of the muscles of the middle ear and different conditions of atmospheric pressure within and without the cavity of the tympanum. Its form is nearly circular. From a number of accurate measurements of its diameter in the adult, by Sappey, we may assume that its ring measures a little more than $\frac{3}{8}$ of an inch vertically and about $\frac{3}{8}$ of an inch antero-posteriorly. The excess of the vertical over the horizontal diameter is about $\frac{1}{25}$ of an inch.[2] Notwithstanding the assertion of some of the older anatomists, that the tympanic membrane presents one or two small perforations, it is now almost universally regarded as forming a complete division, without openings, between the external meatus and the middle ear; or, if any openings exist, they are exceedingly minute.

The periphery of the tympanic membrane is received into a little ring of bone, which may be separated by maceration in early life, but which is consolidated with the adjacent bony structures in the adult. This bony ring is incomplete at its superior portion, but, aside from this, resembles the groove which receives the crystal of a watch. At the periphery of the membrane, is a ring of condensed fibrous tissue, which is received into the bony ring. This ring also presents a break at its superior portion.

The concavity of the membrana tympani presents out-

[1] See p. 155.

[2] Sappey, *Traité d'anatomie*, Paris, 1871, p. 801. The above measurements are given, assuming that the position of the membrane is vertical.

ward, and may be increased or diminished by the action of the muscles of the middle ear. The point of greatest concavity, where the extremity of the handle of the malleus is attached, is called the umbo. Von Tröltsch has described, upon the inner surface of the membrane, two pouches, or pockets. One is formed by a small, irregular, triangular fold situated at the upper part of its posterior half, and consisting of a process of the fibrous layer. This, which is called the posterior pocket, is open below, and extends from the posterior upper border of the membrane to the handle of the malleus, which it assists in holding in position. "After it has been divided, this bone is much more movable than before." The anterior pocket is lower and shorter than the posterior. It is formed by a small bony process turned toward the neck of the malleus, by the mucous membrane, by the bony process of the malleus, by its anterior ligament, the chorda tympani, and the anterior tympanic artery.[1] The handle of the malleus is inserted between the two layers of the fibrous structure of the membrana tympani and occupies the upper half of its vertical diameter, extending from the periphery to the umbo.

The membrana tympani, though thin and translucent, presents three distinct layers. Its outer layer is an excessively delicate prolongation of the integument lining the external meatus, presenting, however, neither papillæ nor glands. The inner layer is a delicate continuation of the mucous membrane lining the tympanic cavity, and is covered by tessellated epithelial cells. The fibrous portion, or lamina propria, is formed of two layers. The outer layer consists of fibres, radiating from the handle of the malleus to the periphery. These are best seen near the centre. The inner layer is composed of circular fibres, which are most abundant near the periphery, and diminish in number toward the centre. Between these two layers, are fusiform corpuscles, described first by Von Tröltsch,[2] which resemble the corneal corpuscles.

[1] Tröltsch, *Diseases of the Ear*, New York, 1869, p. 82. [2] *Loc. cit.*

The color of the membrana tympani, when it is examined with an aural speculum by daylight, is peculiar, and rather difficult to describe, as it varies in the normal ear in different individuals. Politzer describes the membrane, examined in this way, as translucent, and of a color which "most nearly approaches a neutral gray, mingled with a weaker tint of violet and light yellowish-brown."[1] This color is modified, in certain portions of the membrane, by the chorda tympani and the bones of the ear, which produce some opacity. The entire membrane in health has a soft lustre. In addition, there is seen, with proper illumination, a well-marked, triangular cone of light, with its apex at the end of the handle of the malleus, spreading out in a downward and forward direction, and from $\frac{1}{16}$ to $\frac{1}{12}$ of an inch broad at its base. This appearance is regarded by pathologists as very important, as indicating a normal condition of the membrane. It is undoubtedly due to reflection of light, depending upon three factors, indicated by Roosa as follows: "First, the inclination of the membrana tympani to the auditory canal; second, the traction of the malleus, which renders it concave at the centre; third, its polish or brilliancy."[2] With this explanation, it is not admitted that the light spot is due to a peculiar structure of that portion of the membrane upon which it is seen.

Uses of the Membrana Tympani.—It is unquestionable that the membrana tympani is very important in audition. In cases of disease, in which the membrane is thickened, perforated, or destroyed, the acuteness of hearing is always more or less affected. That this is in great part due to the absence of a vibrating surface for the reception of waves of sound, is shown by the relief which is experienced by those patients who can tolerate the presence of an artificial membrane of

[1] POLITZER, *The Membrana Tympani in Health and Disease*, New York, 1869, p. 23.

[2] ROOSA, *Diseases of the Ear*, New York, 1873, p. 189.

rubber, when this is introduced. As regards the mere acuteness of hearing, aside from the pitch of sounds, the explanation of the action of the membrane is very simple. As was shown by Müller,[1] sonorous vibrations are not readily transmitted through the atmosphere to solid bodies, like the bones of the ear; and, when they are thus transmitted, they lose considerably in intensity. When, however, the aërial vibrations are received by a delicate membrane, under the conditions of the membrana tympani, they are transmitted with very little loss of intensity; and if this membrane be connected with solid bodies, like the bones of the middle ear, the vibrations are readily conveyed to the sensory portions of the auditory apparatus. The parts composing the middle ear are thus admirably adapted to the transmission of sonorous waves to the auditory nerves. The membrane of the tympanum is delicate in structure, stretched to the proper degree of tension, and vibrates under the influence of the waves of sound, as has been clearly demonstrated by Savart.[2] Attached to this membrane, is the chain of bones, which conducts its vibrations, like the bridge of a violin, to the liquid of the labyrinth. The membrane is fixed at its periphery and has air on both sides, so that it is under the most favorable conditions for vibration.

A study of the mechanism of the ossicles and muscles of the middle ear shows that the membrana tympani is subject

[1] MÜLLER, *Elements of Physiology*, London, 1843, vol. ii., p. 1248. Müller has investigated very closely the physical laws of the transmission of sonorous vibrations through media of different densities. The following paragraph illustrates the application of these laws to the physiology of the middle ear:

"A small solid body, fixed in an opening by means of a border of membrane, so as to be movable, communicates sonorous vibrations, from air on one side, to water, or the fluid of the labyrinth, on the other side, much better than solid media not so constructed. But the propagation of sound to the fluid is rendered much more perfect if the solid conductor thus occupying the opening (fenestra of the labyrinth) is by its other end fixed to the middle of a tense membrane which has atmospheric air on both sides."

[2] SAVART, *Recherches sur les usages de la membrane du tympan et de l'oreille externe.—Journal de physiologie*, Paris, 1824, tome iv., p. 208, *et seq.*

to certain physiological variations in tension, due to contraction of the tensor tympani. It is also evident that this membrane may be drawn in and rendered tense by exhausting or rarefying the air in the drum. If the mouth and nose be closed and we attempt to breathe forcibly by expanding the chest, the external pressure tightens the membrane. In this condition, Dr. Wollaston has shown that the ear is rendered insensible to grave sounds, but that high-pitched sounds appear to be more intense. If the tension be relieved, as may be done by an act of swallowing, the grave sounds are heard with normal distinctness. This experiment, tried at a concert, produces the curious effect of abolishing a great number of the lowest tones, while the shrill sounds are heard very acutely.[1] The same phenomena are observed when the external pressure is increased by descent in a diving-bell.[2]

Undoubted cases of voluntary contraction of the tensor tympani have been observed by otologists; and in these, by bringing this muscle into action, the limit of the perception of high tones is greatly increased. In two instances of this kind, recorded by Dr. Blake, of Boston, the ordinary limit of perception was found to be three thousand single vibrations; and, by contraction of the muscle, this was increased to five thousand single vibrations.[3]

The admirable experiments of Savart, to which we have already alluded, show that the membrana tympani vibrates

[1] WOLLASTON, *On Sounds inaudible by Certain Ears.—Philosophical Transactions*, London, 1820, p. 306, *et seq.*

[2] TODD, *Cyclopædia of Anatomy and Physiology*, London, 1836–1839, vol. ii., p. 575, Article, *Hearing.*

[3] BLAKE, *Summary of Results of Experiments on the Perception of High Musical Tones.—Trans. of the American Otological Society*, Boston, 1872, vol. v., p. 77.

Other cases of voluntary contraction of the tensor tympani have been observed. Schapringer, who possessed this faculty, was able to contract the muscle so as to render all notes below seventy vibrations inaudible, while the higher tones were more readily perceived the more energetic the tension of the membrane. (*Ueber die Contraction des Trommelfellspanners.—Sitzungberichte der kaiserlichen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Classe*, Wien, 1870, Bd. lxii., Zweite Abtheilung, S. 572.)

by influence, when it is brought in accord with a given tone. In other words, this membrane obeys the laws of consonance, and vibrates strongly by the influence of sounds in unison or in harmony with its fundamental tone. The laws of vibrations by influence have been fully discussed in the preceding chapter;[1] and it remains for us now to determine how far these laws are applicable to the physiology of the vibrations of the membrana tympani, and the action of these vibrations in the accurate perception of musical sounds.

There are certain phenomena of vibration of the membrana tympani that must occur, as a physical necessity, under favorable conditions, which it is important to note in this connection; and these have hardly attracted sufficient attention at the hands of physiological writers. In the first place, this membrane must obey the laws of vibration by influence. It is undoubtedly thrown into vibration by irregular waves of noise, as contradistinguished from musical tones; but when a tone is sounded in unison with its fundamental tone, or when the tone sounded is one of the octaves of its fundamental, it must undergo a vibration by influence, like an artificial membrane. If we suppose the membrane to be tuned in unison with a certain tone, it will not only return this tone by influence, but will repeat its quality. Not only this, when a combination of harmonious tones is sounded, the combined sound will be returned, with all the shades in quality which the combined tones produce. On account of its small size, the sound produced by the exposed membrane itself cannot be heard; but that the membrane does vibrate by influence, has been proven by experiments with small particles of sand on its surface.

We are certainly justified in supposing that vibrations of the membrana tympani, too delicate to be revealed to the eye or the ear in objective experiments, may be appreciated by the auditory nerves as a subjective phenomenon. In other words, we can probably appreciate vibrations in our own tym-

[1] See page 192.

panic membrane, when these would be too delicate to be observed by the eye or ear, in a membrane exposed and subjected to similar influences. This point must be accepted as probable; and it cannot be proven by direct experiment. If this be true, the most complex combinations of sound produced by an orchestra might be actually reproduced by the tympanic membrane, if this membrane were accurately tuned to the fundamental tone.

The arrangement of the muscles and bones of the middle ear admits of the possibility of tuning the membrana tympani with exquisite nicety. These muscles are sometimes so far under the control of the will that we can tighten the membrane to its limit by a voluntary effort; the muscles are of the striated variety, and are capable of rapid action; they are supplied with motor filaments from the cerebrospinal system; the ear is fatigued by long attention to particular tones; persons not endowed with what is termed a musical ear cannot appreciate slight distinctions between different tones; the ear is capable of education in the appreciation of pitch and in following rapid successions of tones; and, in short, there are many points in the mechanism of the transmission of musical sounds in the ear that seem to involve muscular action. In the larynx, we are conscious of differences in the tension of the vocal cords only from differences in the character and pitch of the sounds produced; in the eye, we are conscious of the contraction of the muscle of accommodation from the fact that an effort enables us to see objects distinctly at different distances; and it is not impossible that, under ordinary conditions, the consciousness of contractions of the muscles of the middle ear may be revealed only by the fact of the correct appreciation of certain musical tones. Some persons can educate the ear so as to acquire what is called the faculty of absolute pitch; that is, without the aid of a tuning-fork or any musical instrument, they can give the exact musical value of any given tone. A possible explanation of this is that such persons may have educated

the muscles of the ear so as to put the tympanic membrane in such a condition of tension as to respond to a given note and to recognize the position of this note in the musical scale. Finally, an accomplished musician, in conducting an orchestra, can, by a voluntary effort, direct his attention to certain instruments, and hear their notes distinctly, separating them, as it were, from the general mass of sound, can distinguish the faintest discords, and immediately designate a single instrument making a false note.

The fact that rapid successions of notes are readily appreciated does not of necessity argue against the possibility of following these notes with the muscles of the ear; for the muscles of the larynx may act so as to produce successions of notes as rapidly as they can be correctly appreciated. Nor does the fact that we must prepare the tympanic membrane for certain notes militate against the theory we have just given, for musical compositions present melodious successions in a certain scale, the notes of which bear well-defined harmonious relations to each other, and we immediately appreciate a change in the key, which is simply a change in the fundamental. These changes in the key must be made in accordance with the laws of modulation; otherwise they are harsh and grating. Modulation in music is simply a mode of passing from one key to another by certain transition-notes or chords, which seem inevitably to lead to a certain key, and to no other. Finally, the laws of vibration by influence show that a single vibrating membrane returns the quality as well as the pitch of tones and combinations of tones as well.

The theory we have just given of the possible action of the membrana tympani is an elaboration of the view advanced by Everard Home.[1] Unfortunately for the simplicity of the mechanism of hearing and the idea of division and

[1] HOME, *On the Organ of Hearing.—Lectures on Comparative Anatomy*, London, 1823, vol. iii., p. 268, *et seq.* In this article, there was no experimental proof given of the theory advanced, and it does not seem that the laws of vibration by influence were fully recognized. The author erred, also, in assuming that the membrana tympani itself is a muscular membrane. It is probably for these

isolation of function in different parts, which is so seductive to physiologists, there are certain facts and considerations which prevent us from adopting it absolutely and exclusively as an explanation of the mechanism of the appreciation of musical sounds. These are the following:

Destruction of both membranæ tympani does not necessarily produce total deafness, although this condition involves considerable impairment of hearing. So long as there is simple destruction of these membranes, the bones of the middle ear and the other parts of the auditory apparatus being intact, the waves of sound are conducted to the auditory nerves, though imperfectly. In a remarkable case reported by Sir Astley Cooper, which is cited by most writers on physiology, one membrana tympani was entirely destroyed, and the other was nearly gone, there being some parts of its periphery remaining. In this person, the hearing was somewhat impaired, though he could distinguish ordinary conversation pretty well. Fortunately he had considerable musical taste, and it was ascertained that his musical ear was not seriously impaired; "for he played well on the flute and had frequently borne a part in a concert. I speak this, not from his authority only, but also from that of his father, who is an excellent judge of music, and plays well on the violin: he told me, that his son, besides playing on the flute, sung with much taste, and perfectly in tune."[1] This single case, if its details be accurate—which we have no reason to doubt—shows conclusively that the correct appreciation of musical sounds may exist independently of the action of the membrana tympani.

There is now one consideration, of the greatest importance, that must be kept in view in studying the functions of

reasons that the theory has received so little consideration by later writers. It is interesting, however, to note several cases reported by Home, in which the correct appreciation of musical sounds was temporarily lost, in some cases, as the result of a nervous affection, and in others, from catarrh.

[1] COOPER, *Observations on the Effects which take place from the Destruction of the Membrana Tympani of the Ear. In a Letter to* EVERARD HOME.—*Philosophical Transactions*, London, 1800, p. 155.

any distinct portion of the auditory apparatus, like the membrana tympani. This, like all other parts of the apparatus, except the auditory nerves themselves, has simply an accessory function. If the regular waves of a musical tone be conveyed to the terminal filaments of the auditory nerves, these waves make their impression and the tone is appreciated. It makes no difference, except as regards intensity, how these waves are conducted; the tone is appreciated by the impression made upon the nerves, and the nerves only. The waves of sound are not like the waves of light, refracted, decomposed, perhaps, and necessarily brought to a focus as they impinge upon the retina; as far as the action of the accessory parts of the ear are concerned, the waves of sound are unaltered; that is, the rate of their succession remains absolutely the same, though they be reflected by the concavities of the concha, and repeated by the tympanic membrane. Even if we assume that the membrane, under normal conditions, repeats musical sounds by vibrations produced by influence, and that this membrane is tuned by voluntary muscular action so that tones are exactly repeated, the position of these tones in the musical scale is not and cannot be altered by the action of any of the accessory organs of hearing. The fact that a person may retain his musical ear with both membranes destroyed is not really an argument against the view that the membrane repeats tones by influence; for, if musical tones or noisy vibrations be conducted to the auditory nerves, the impression produced must of necessity be dependent exclusively upon the character, regularity, and number of the sonorous vibrations. And, again, the physical laws of sound, which are fixed and unchangeable, teach us that a membrane, like the membrana tympani, must return or reproduce sounds which are in unison or are harmonious with its fundamental tone, much more perfectly than discordant or irregular vibrations. In a loud confusion of noisy sounds, we can readily distinguish pure melody or harmony, even when the vibrations of the latter are compara-

tively feeble. In following with the ear any piece of music, reasoning from purely physical considerations, it must at times occur that the tones are in exact unison or in harmony with the fundamental tone of the membrana tympani. Supposing the fundamental tone of the membrane to be constant and invariable, such tones would be heard much more distinctly than others, as a physical necessity. Such a difference in the appreciation of certain notes in melody does not occur; and the only reasonable explanation of this is that the tension of the membrane is altered. It is shown by anatomical researches that the tension can be altered by muscular action, and, as the muscles are striated, we may suppose that it may be modified rapidly. Physiological observations show that such modifications in tension do occur; and there are on record unquestionable instances in which the membrana tympani is tightened by a voluntary contraction of the tensor-tympani muscle.[1]

Another important point to note in this connection is the following: Can it be shown that the appreciation of the pitch of tones bears any relation to the degree of tension of the tympanic membrane? We can answer this question unreservedly in the affirmative. When the membrane is rendered tense, there is insensibility to low tones. When the membrane is brought to the highest degree of tension by voluntary contraction of the tensor tympani, the limit of appreciation of high tones may be raised from three thousand to five thousand vibrations. It is a fact in the physics of the membrana tympani, that the vibrations are more intense the nearer the membrane approaches to a vertical position. It has also been shown that the membrane has a strikingly vertical position in musicians, and that the position is very oblique in persons with an imperfect musical ear.[2] This fact has a most important bearing on the probable relation between the membrana tympani and the correct appreciation of musical sounds.

[1] See page 201. [2] Tröltsch, *Diseases of the Ear*, New York, 1869, p. 36.

In view of all facts and considerations for and against the theory which we have given of the action of the tympanic membrane in the appreciation of musical sounds, does it not seem probable that there are, acting upon this membrane, muscles of auditory accommodation, analogous in their operation to the muscle of visual accommodation? We have carefully studied this subject in all its bearings, and, if the reader follow closely our process of reasoning, it must seem probable that the muscles of the middle ear are muscles of auditory accommodation; but it should be remembered that the action of the membrane is not absolutely essential, and that musical tones, however conducted, must of necessity be correctly appreciated, whenever and however they find their way to the auditory nerves.[1]

Experiments, to which we have already referred in another volume,[2] have shown pretty conclusively that the tympanic membrane vibrates more forcibly when relaxed than when it is tense. It is evident that the relaxed membrane must undergo vibrations of greater amplitude than when it is under strong tension. In certain cases of facial palsy, in which it is probable that the branch of the facial going to the tensor tympani was affected, the ear became painfully sensitive to powerful impressions of sound. This probably has no relation to pitch, and most sounds that are painfully loud are comparatively grave. The tension of the membrane may be modified as a means of protection of the ear, but the facts belonging to cases of facial palsy are all that we have

[1] Bonnafont has proposed a theory of the action of the membrana tympani in audition, in which the membrane is supposed to undergo partial tensions and relaxations, and thus to bring certain portions of it in unison with different tones. It is difficult to see how this could be demonstrated, even should it occur; and it is easier to explain the appreciation of harmonious combinations of tones, by the well-known laws regulating the vibrations of membranes by influence. (BONNAFONT, *Traité théorique et pratique des maladies de l'oreille*, Paris, 1873, p. 277.) Bonnafont published a memoir, in which the above-mentioned theory was proposed, in 1859.

[2] See vol. iv., Nervous System, p. 155.

bearing upon this point. Artillerists are in danger of rupture of the membrana tympani from sudden concussions. To guard against this injury, it is recommended to stop the ear, draw the shoulder up against the ear most in danger, and particularly to inflate the middle ear after Valsalva's method. "This method consists in making a powerful expiration, with the mouth and nostrils closed."[1]

Mechanism of the Ossicles of the Ear.—The ossicles of the middle ear, in connection with the muscles, have a twofold function: First, by the action of the muscles, the membrana tympani may be brought to different degrees of tension. Second, the chain of bones serves to conduct sonorous vibrations to the labyrinth. It must be remembered that the handle of the malleus is closely attached to the membrana tympani, especially near its lower end. Near the short process, the attachment is looser and there is even an incomplete joint-space at this point. The long process is attached closely to the Glasserian fissure of the temporal bone.

The malleus is articulated with the incus by a very peculiar joint, which has been accurately described by Helmholtz. This joint is so arranged, presenting a sort of cog, that the handle of the malleus can rotate only outward; and when a force is applied which would have a tendency to produce a rotation inward, the malleus must carry the incus with it. This mechanism has been aptly compared by Helmholtz to that of a watch-key with cogs which are fitted together and allow the whole key to turn in one direction, but are separated so that only the upper portion of the key turns when the force is applied in the other direction.[2] In the articula-

[1] TRÖLTSCH, *Diseases of the Ear*, New York, 1869, p. 148. According to Dr. Roosa, rupture of the tympanic membrane has been very seldom observed in soldiers during the late war in this country, though it is well known that it sometimes occurs, even from the report of a pistol near the ear. (ROOSA, *Diseases of the Ear*, New York, 1873, p. 223.)

[2] HELMHOLTZ, *Mechanism of the Ossicles of the Ear and Membrana Tympani*, New York, 1873, p. 32, *et seq.*

tion between the malleus and the incus, the only difference is that there is but one cog; but this is sufficient to prevent an independent rotation of the malleus inward. This enables us to understand the action of the tensor-tympani muscle. By the contraction of this muscle, "all the bands which give firmness to the position of the ossicles are rendered tense. This muscle, in the first place, draws the handle of the hammer inward, and with it the membrana tympani. At the same time it pulls upon the axis-band of the hammer, drawing it inward and putting it upon the stretch. Another effect, as we have shown, is to draw the head of the hammer away from the tympano-incudal joint, to tighten all the ligaments of the anvil, those toward the hammer as well as those at the end of its short process, and to lift the latter up from its bony bed. In this way the anvil is brought into the position where the cogs of the malleo-incudal joint fit into one another the tightest. Finally, the long process of the anvil is compelled to perform a rotation inward in company with the handle of the hammer; in so doing, as we shall see further on, it presses upon the stirrup and drives it into the oval window against the fluid of the labyrinth.

"In this respect the construction of the ear is very remarkable. By the contraction of the single mass of elastic fibres constituting the tensor tympani (whose tension, besides, is variable and may be adapted to the wants of the ear) all the inelastic tendinous ligaments of the ossicles are simultaneously put upon the stretch."[1]

The body of the incus is attached to the posterior bony wall of the tympanic cavity. Its articulation with the malleus has just been indicated. By the extremity of its long process, it is also articulated with the stapes, which completes the chain. *In situ*, the stapes forms nearly a right angle with the long process of the incus.

The stapes is articulated with the incus, as indicated above,

[1] HELMHOLTZ, *Mechanism of the Ossicles of the Ear and Membrana Tympani*, New York, 1873, p. 40.

and its oval base is applied to the fenestra ovalis. Surrounding the base of the stapes, is a ring of elastic fibro-cartilage, which is closely united to the bony wall of the labyrinth, by an extension of the periosteum over the base of the stapes.

"The relation of the stirrup to the anvil is such that, if the handle of the hammer be drawn inward, the long process of the anvil presses firmly against the knob of the stirrup; the same takes place if the capsular ligament between both be cut through."[1]

The articulations between the malleus and the incus and between the incus and the stapes are so arranged that when the membrana tympani is forced outward, as it may be by inflation of the tympanic cavity, there is no danger of tearing the stapes from its attachment to the fenestra ovalis; for, when the handle of the malleus is drawn outward, the cog-joint between the malleus and the incus is loosened and no great traction can be exerted upon the stapes.

The fact that the stapes may be pressed against the liquid of the labyrinth was demonstrated by a very satisfactory experiment described by Helmholtz, in which an opening, made into the superior semicircular canal, was fitted with a slender glass tube, and the vestibule and a portion of the tube filled with water. "The movements of the bones of the ear produced by forcing air into the external meatus caused the fluid in the tube to rise 0·9 mm." From this experiment, it was calculated that the excursions of the stapes amounted to from $\frac{1}{450}$ to $\frac{1}{850}$ of an inch.[2]

Although the experiments which we have cited illustrate pretty conclusively the mechanism of the ossicles and the action of the tensor-tympani muscle, both as regards the chain of bones and the membrana tympani, direct observations

[1] HELMHOLTZ, *op. cit.*, p. 48.

[2] *Op. cit.*, p. 43.

The movements of the stapes have been described by Dr. A. H. Buck, in an elaborate paper. The details of his experiments, however, are very minute, and the facts stated above are sufficient for our purpose. (BUCK, *On the Mechanism of the Ossicles of the Ear*, New York, 1870.)

are wanting to show the exact relations of these different conditions of the ossicles and of the membrane to the physiology of audition. One very important physical point, however, which has been the subject of much discussion, is settled. The chain of bones acts as a single solid body in conducting vibrations to the labyrinth.[1] It is a matter of physical demonstration that vibrations of the bones themselves would be infinitely rapid as compared with the highest tones which can be appreciated by the ear, if it were possible to induce in these bones regular vibrations. Practically, then, the ossicles have no independent vibrations that we can appreciate. This being the fact, the ossicles simply conduct to the labyrinth the vibrations induced in the membrana tympani by sound-waves; and their arrangement is such that these vibrations lose very little in intensity. While it has been shown experimentally, by Politzer and others, that the amplitude of vibration in the membrana tympani and the ossicles diminishes with the tension of the membrane,[2] it would seem that, when the tensor tympani contracts, it must render the conduction of sound-waves to the labyrinth more delicate than when the auditory apparatus is in a relaxed condition, which we may compare with the "indolent" condition of the apparatus of accommodation of the eye. When the membrana tympani is relaxed and the cog-like articulation between the malleus and the incus is loosened, the vibrations of the membrane and of the malleus may have a greater amplitude; but, when the malleo-incudal joint is tightened and the stapes is pressed against the fenestra ovalis, the loss of intensity of vibration in conduction through the bones to the labyrinth must be reduced to the minimum. With this view, the tensor-tympani muscle, while it contracts to secure for

[1] Helmholtz (*op. cit.*) demonstrated the mechanism of the malleo-incudal joint, and showed how the bones conduct vibrations as a single solid lever; but he gives full credit to Weber (p. 8), who first proposed this theory, though it was defective from his want of knowledge of the exact mode of articulation of the bones.

[2] Politzer, *Untersuchungen über Schallfortpflanzung und Schallleitung im Gehörgane.—Archiv für Ohrenheilkunde*, Würzburg, 1864, Bd. i., S. 68, *et seq.*

the membrana tympani the degreee of tension most favorable for vibration under the influence of certain tones, puts the chain of bones in the condition best adapted to the conduction of the vibrations of the membrane to the labyrinth, with the smallest possible loss of intensity.

Physiological Anatomy of the Internal Ear

The internal ear consists of the labyrinth, which is divided into the vestibule, semicircular canals, and cochlea. The general arrangement of these parts has already been described;[1] and it only remains for us to study the structures contained within the bony labyrinth, in so far as their anatomy bears upon the physiology of audition. The most delicate and complicated points, by far, in the anatomy of the auditory apparatus are connected with the histology of the internal ear, which, since the researches of Corti, has been studied very closely, particularly in Germany. We shall avoid, however, the discussion of histological questions of purely anatomical interest, and confine ourselves to those points which have a direct bearing upon physiology.

Passing inward from the tympanum, the first division of the internal ear is the vestibule. This cavity communicates with the tympanum by the fenestra ovalis, which is closed in the natural state by the base of the stapes. It communicates, also, with the semicircular canals and with the cochlea.

General Arrangement of the Membranous Labyrinth.—The bony labyrinth is lined by a moderately-thick periosteum, consisting of connective tissue, a few delicate elastic fibres, numerous nuclei, and blood-vessels, with spots of calcareous concretions. This membrane adheres closely to the bone and extends over the fenestra ovalis and the fenestra rotunda. Its inner surface is smooth and covered with a single layer of cells of pavement-epithelium, in some parts being segmented and in others forming a continuous nucleated sheet. In certain

[1] See page 163.

portions of the vestibule and semicircular canals, the periosteum is united to the membranous labyrinth, more or less closely, by fibrous bands, which have been called ligaments of the labyrinth.[1] The fenestra rotunda, which lies between the cavity of the tympanum and the cochlea, is closed by a membrane formed by an extension of the periosteum lining the cochlea, on the one side, and the mucous membrane lining the tympanic cavity, on the other.

In the bony vestibule, occupying about two-thirds of its cavity, are two distinct sacs; a large, ovoid sac, the utricle, situated in the upper and posterior portion of the cavity, and a smaller, rounded sac, the saccule, situated in its lower and anterior portion. The utricle communicates with the semicircular canals; and the saccule opens into the membranous canal of the cochlea by the canalis reuniens. At a point in the utricle corresponding to the entrance of a branch of the auditory nerve, is a round, whitish spot, called the acoustic spot (macula acustica), containing otoliths, or otoconia, which are attached to the inner surface of the membrane. A similar spot, containing otoliths, exists in the saccule at the point of entrance of its nerve. Otoliths are also found in the ampullæ of the semicircular canals. These calcareous masses are composed of crystals of carbonate of lime, hexagonal and pointed at their extremities. According to Sappey, each crystal corresponds to a nerve-fibre.[2] Nothing definite is known of the function of these calcareous bodies, which exist in man, mammals, birds, and reptiles.

The membranous semicircular canals occupy about one-third of the cavity of the bony canals. They present little ovoid dilatations, ampullæ, corresponding to the ampullary enlargements of the bony canals.

The membrane of the cochlea, including the lining periosteum, occupies the spiral canal of the cochlea, which it fills

[1] Rüdinger, in Stricker, *Manual of Human and Comparative Histology*, The New Sydenham Society, London, 1873, vol. iii., p. 88.

[2] Sappey, *Traité d'anatomie*, Paris, 1871, tome iii., p. 842.

completely. Viewed externally, it appears as a single tube, following the turns of the bony cochlea, beginning below, at the first turn, by a blind extremity, and terminating in a blind extremity at the summit of the cochlea. If we make a section of the cochlea, in a direction vertical to its coils, it will be seen that this canal is divided, partly by bone and partly by membrane, into an inferior portion, a superior portion, and a triangular canal, lying between the two, which is external. The bony septum is in the form of a spiral plate, extending from the central column, the modiolus, into the cavity of the cochlea, about half-way to its external wall, and terminating above in a hook-shaped extremity, called the hamulus. The free edge of this bony lamina is thin and dense. Near the central column, it divides into two plates, with an intermediate spongy structure, in which are lodged vessels and nerves. The surface of the bony lamina looking toward the base of the cochlea is marked by numerous regular, transverse ridges, or striæ.

Attached to the free margin of the bony lamina, is a membrane, the membrana basilaris, which extends to the outer wall of the cochlea. In this way, the canal of the cochlea is divided into two portions, one above and the other below the septum. The portion below begins at the fenestra rotunda, and is called the scala tympani. The portion above, exclusive of the triangular canal of the cochlea, communicates with the vestibule, and is called the scala vestibuli.

Above the membrana basilaris, is a membrane, the limbus laminæ spiralis, the external continuation of which is called the membrana tectoria, or the membrane of Corti. Between the membrana tectoria and the membrana basilaris, is the organ of Corti. The membrane of Reissner extends from the inner portion of the limbus upward and outward to the outer wall of the cochlea. This divides the portion of the cochlea situated above the scala tympani into two portions, an internal portion, the scala vestibuli, and an external, trian-

gular canal, called the canalis cochleæ, or the membranous cochlea.

In the anatomical description of the contents of the bony cochlea, the membranous parts may be designated as follows:

1. The portion below the bony and membranous septum, called the scala tympani. This is formed by the periosteum lining that portion of the cochlea and the under surface of the bony lamina, and the membrana basilaris.

2. The scala vestibuli. This is formed by the periosteum lining the corresponding portion of the bony cochlea and

FIG. 15.

Vertical section of the cochlea of a fœtal calf, magnified six diameters. This section shows the septum between the two scalæ, the scala tympani below the septum, the scala vestibuli above the septum, and the triangular canal externally. The outer wall of the cochlea is ossified, but the modiolus is still cartilaginous. The radiating lines in the modiolus indicate the course of the auditory nerves. (KÖLLIKER, *Handbuch der Gewebelehre*, Leipzig, 1867, S. 714.)

the upper surface of the bony septum, and is bounded externally by the membrane of Reissner.

3. The true, membranous cochlea. This is the spiral triangular canal, bounded externally by the periosteum of the corresponding portion of the wall of the cochlea; internally, by the membrane of Reissner; and, on the other side, by the membrana basilaris.[1] What we thus call the membra-

[1] Some anatomists include this canal in the scala vestibuli. For the sake of clearness, we describe it by itself, as a distinct canal.

nous cochlea is divided by the limbus laminæ spiralis and the membrana tectoria into two portions; a triangular canal above, which is the larger, and a quadrilateral canal below, between the limbus and membrana tectoria and the membrana basilaris. The quadrilateral canal contains the organ of Corti and various structures of a very complicated character. The relations of these divisions of the cochlea, a knowledge of which is essential to the comprehension of the physiological anatomy of this portion of the auditory apparatus, are shown in Fig. 15, with the exception of the quadrilateral canal, which will be shown in another figure.

FIG. 15.

1, *scala tympani*; 2, *scala vestibuli*; 3, *triangular canal*; 4, *quadrilateral canal, called the canal of Corti*; 5, 5, spiral ligament; 6, middle, or angular portion of the spiral ligament giving attachment to the membrana basilaris; 7, portion of the spiral ligament giving attachment to the membrana tectoria, or membrane of Corti; 8, external spiral groove; 9, anterior extremity of the spiral ligament, giving attachment to the membrane of Reissner; 10, *membrane of Reissner*; 10′, vascular band, the outer boundary of the triangular canal; 11, membrane of Corti; 12, *membrana basilaris*; 13, spiral vessel below the membrana basilaris; 14, sulcus spiralis; 15, anterior portion of the band marked by furrows; 16, posterior portion; 17, anterior margin; 18, posterior margin; 19, *the two pillars of the organ of Corti*; 20, branch of the cochlear nerve; 21, spiral ganglion; 22, continuation of the nerve; 23, one of the orifices by which the nerve passes to the organ of Corti; 24, 24, bony tissue of the cochlea; 25, 25, *periosteum*. (SAPPEY, *Traité d'anatomie*, Paris, 1871, tome iii., p. 845.) The parts which have been described in the text are indicated by italics.

The membranous cochlea, as described above, follows the spiral course of the cochlea, terminates superiorly in a blind, pointed extremity at the cupola, beyond the hamulus, and is connected below with the saccule of the vestibule by the canalis reuniens. The relations of the different portions of the membranous cochlea to each other and to the scalæ of the cochlea are shown in Fig. 16. This figure also shows other structures, which we shall not describe more minutely, as they are of purely anatomical interest.

We shall now describe, as possessing the most physiological interest, the liquids of the labyrinth, the distribution and connections of the nerves in the labyrinth, and the organ of Corti.

Liquids of the Labyrinth.—The labyrinth contains a certain quantity of a clear, watery liquid, called the humor of Cotugno, or of Valsalva. A portion of this liquid surrounds the membranous sacs of the vestibule, the semicircular canals, and the membranous cochlea, and this is known as the perilymph of Breschet. Another portion of the liquid fills the membranous labyrinth. This is sometimes called the humor of Scarpa, but is known more generally as the endolymph of Breschet.[1] The perilymph occupies about one-third of the cavity of the vestibule, of the semicircular canals and both scalæ of the cochlea. Both this liquid and the endolymph are clear and watery, becoming somewhat opalescent on the addition of alcohol. The perilymph seems to be secreted by the periosteum lining the osseous labyrinth. As far as we know, the uses of the liquid of the internal ear are to sustain the delicate structures contained in this portion of the auditory apparatus and to conduct sonorous vibrations to the terminal filaments of the auditory nerves and the parts with which they are connected.

Distribution of the Nerves in the Labyrinth.—As the

[1] BRESCHET, *Recherches anatomiques et physiologiques sur l'organe de l'ouïe et sur l'audition*, Paris, 1836, pp. 51, 56.

auditory nerves enter the internal auditory meatus, they divide into an anterior, or cochlear, and a posterior, or vestibular branch. The vestibular branch divides into three smaller branches, a superior and anterior, a middle, and a posterior branch. The superior and anterior branch, the largest of the three, is distributed to the utricle, the superior semicircular canal, and the external semicircular canal. The middle branch is distributed to the saccule. The posterior branch passes to the posterior semicircular canal. The nerves distributed to the utricle and saccule penetrate at the points occupied by the otoliths, and the nerves going to the semicircular canals pass to the ampullæ, which also contain otoliths. In each ampulla, at the point where the nerve enters, is a transverse fold, projecting into the canal and occupying about one-third of its circumference, called the septum transversum.

The nerves terminate in essentially the same way in the sacs of the vestibule and the ampullæ of the semicircular canals. At the points where the nerves enter, in addition to the otoliths, are cells of cylindrical epithelium, of various forms, which pass gradually into the general pavement-epithelium of the cavities. In addition to these cells, are fusiform, nucleated bodies, the free ends of which are provided with hair-like processes, called fila acustica. These are about $\frac{1}{800}$ of an inch in length, and are distributed in quite a regular manner around the otoliths. The nerves form an anastomosing plexus beneath the epithelium, and probably terminate in the fusiform bodies just described as presenting the fila acustica at their free extremities. In the sacs of the vestibule and in the semicircular canals, nerves exist only in the macula acustica and the ampullæ.

The cochlear division of the auditory nerve breaks up into numerous small branches, which pass through foramina at the base of the cochlea, in what is called the tractus spiralis foraminulentus. These follow the axis of the cochlea and pass, in their course toward the apex, between the plates of the bony spiral lamina. Between these plates of bone, the dark-bor-

dered nerve-fibres pass each one through a bipolar cell, these cells together forming a spiral ganglion, known as the ganglion of Corti. Beyond this ganglion, the nerves form an anastomosing plexus, and finally enter the quadrilateral canal, or the canal of Corti. As they pass into this canal, they suddenly become pale and exceedingly fine, and probably are connected finally with the organ of Corti, though their exact mode of termination has not yet been determined. The

FIG. 17.

Distribution of the cochlear nerve in the spiral lamina of the cochlea (the cochlea is from the right side, and is seen from its antero-inferior part).—1, trunk of the cochlear nerve; 2, 2, 2, membranous zone of the spiral lamina; 3, 3, 3, terminal expansion of the cochlear nerve exposed in its whole extent by the removal of the superior plate of the lamina spiralis; 4, orifice of communication of the scala tympani and the scala vestibuli. (SAPPEY, *Traité d'anatomie*, Paris, 1871, tome iii., p. 854.)

course of the nerve-fibres to their distribution in the cochlea is shown in Fig. 17. 21, Fig. 16, shows the ganglion of Corti, and 23, the point of penetration of the nerve into the canal of Corti.

Organ of Corti.—Of all the parts contained within the bony labyrinth, the organ of Corti possesses the greatest physiological interest; for it is this organ which is supposed to receive the sonorous vibrations and communicate them directly to the terminal filaments of the auditory nerves. Al-

though this view has not received the support of actual demonstration, it affords an explanation, more or less plausible, of the mechanism of audition, carried to the point of the actual reception of impressions by the nerves. In view of this, it is important to have a clear comprehension of the arrangement of those parts which are supposed to receive the sonorous vibrations; and we shall, for the sake of simplicity, eliminate from our description certain accessory structures, the functions of which are obscure.

In the quadrilateral canal, bathed in the endolymph, throughout its entire spiral course, is an arrangement of pillars, or rods, regular, like the strings of a harp in miniature, which are supposed to repeat the varied vibrations of sound. These are the pillars of Corti.[1]

The structures contained in the quadrilateral canal are so delicate that their investigation presents great difficulty; but the arrangement of the pillars, or rods of Corti is pretty well understood. These pillars are external and internal, with their bases attached to the basilar membrane, and their summits articulated above, so as to form a regular, spiral arcade, enclosing a triangular space, which is bounded below by the basilar membrane. The number of the elements of the organ of Corti is estimated at about 3,500, for the outer, and 5,200, for the inner rods, the proportion of inner rods to the outer being about three to two.[2] The relations of these structures to the membranous labyrinth are seen in Fig. 16, (19). In this figure, it is seen that the internal pillar, which is the shorter of the two, is attached to the basilar membrane just external to the point of entrance of the nerve into the quadrilateral canal. The external pillar is longer, more delicate and rounded, and is also attached to the basilar membrane. The form of the pillars is more exactly shown in

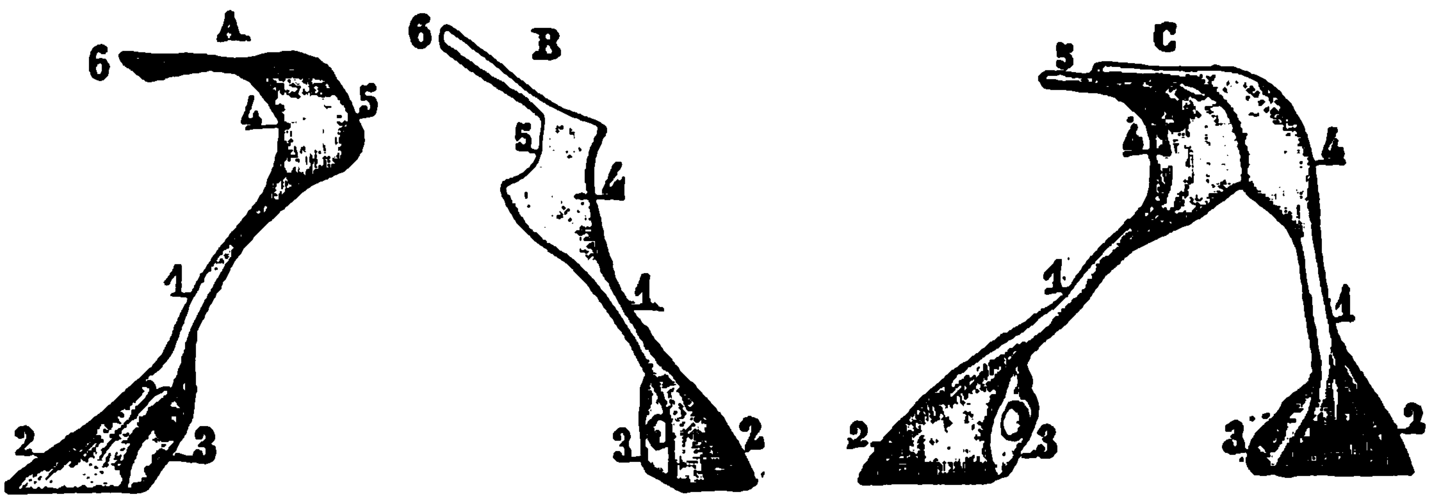
[1] CORTI, *Recherches sur l'organe de l'ouïe des mammifères*, 1851, p. 15, *et seq.*

[2] PRITCHARD, *On the Structure and Functions of the Rods of the Cochlea in Man and other Mammals.—Proceedings of the Royal Society*, London, 1872, vol. xx., p. 371.

Figs. 18 and 19, the latter figure, however, exhibiting other structures which enter into the constitution of the organ of Corti. It will be remarked that a small nucleated body is attached to the base of each pillar. At the summit, where the internal and the external pillars are joined together, is a delicate prolongation, directed outward, which is attached to the covering of the quadrilateral canal.

The above description comprises about all that is definitely known of the arrangement of the pillars, or rods of Corti. They are nearly homogeneous, except when treated with reagents, and are said to be of about the consistence of

FIG. 18.



The two pillars of the organ of Corti:
A, External pillar of the organ of Corti.—1, body, or middle portion; 2, posterior extremity, or base; 3, cell on its internal side; 4, anterior extremity; 5, convex surface by which it is joined to the internal pillar; 6, prolongation of this extremity.
B, Internal pillar of the organ of Corti.—1, body, or middle portion; 2, posterior extremity; 3, cell on its external side; 4, anterior extremity; 5, concave surface by which it is joined to the external pillar; 6, prolongation, subjacent to that of the external pillar.
C, The two pillars of the organ of Corti, united by their anterior extremity, and forming an arcade, the concavity of which presents outward.—1, 1, body, or middle portion of the pillars; 2, 2, posterior extremities; 3, 3, cells attached to the posterior extremities; 4, 4, anterior extremities joined together; 5, terminal prolongation of this extremity. (SAPPEY, *Traité d'anatomie*, Paris, 1871, tome iii., p. 849.)

cartilage.[1] They are closely set together, with very narrow spaces between them, and it is difficult to see how they can be stretched to any considerable degree of tension. The arch is longer at the summit than at the base of the cochlea, the longest rods, at the summit, measuring about $\frac{1}{200}$ of an inch, and the shortest, at the base, about $\frac{1}{500}$ of an inch.[2] As we

[1] QUAIN, *Elements of Anatomy*, London, 1867, vol. ii., p. 765.

[2] The measurements given above are taken from a recent article by Pritchard,

before remarked, the relations between the pillars and the terminal filaments of the auditory nerves are not definitely settled.

In addition to the pillars just described, various cellular elements enter into the structure of the organ of Corti. The most important of these are the inner and the outer hair-cells. The inner hair-cells are arranged in a single row, and the outer hair-cells, in three rows. Nothing definite is known

FIG. 19.

Vertical section of the organ of Corti of the dog. Magnified 800 diameters.
a–b, homogeneous layer of the basilar membrane; *v*, tympanic layer, with nuclei, granular cell-protoplasm, and connective tissue; a_1, tympanic lip of the crista spiralis; *c*, thickened portion of the basilar membrane; *d*, spiral vessel; *e*, blood-vessel; *f*, bundle of nerves; *g*, epithelium; *i*, inner hair-cell, with its basilar process, *k*; *l*, head-plate of the inner pillar; *m*, union of the two pillars; *n*, base of the inner pillar; *o*, base of the outer pillar; *p*, *q*, *r*, outer hair-cells, with traces of the cilia; *t*, bases of two other hair-cells; *s*, Hensen's prop-cell; $l–l_1$, lamina reticularis; *w*, nerve-fibre passing to the first hair-cell, *p*. (WALDEYER, in STRICKER, *Handbuch der Lehre von den Geweben*, Leipzig, 1871, S. 944.)

of the function of these cells. The relations of these parts are shown in Fig. 19, which is rather complex, but, on careful study, gives a good idea of the arrangement of all of the structures which compose the organ of Corti. It is supposed

already referred to. At the base of the cochlea, the two sets of rods are about equal in length. From the base to the apex, both sets, outer and inner, progressively increase in length, and the outer rods become the longer, so that, near the apex, they are nearly twice the length of the inner.

by some anatomists that the filaments of the auditory nerves terminate in the cells above described; but this point is not definitively settled.

Functions of Different Parts of the Internal Ear.

The precise function of the different parts which are found in the internal ear is obscure, notwithstanding the careful researches that have been made into the anatomy and the physiology of the labyrinth. There are several points, however, bearing upon the physiology of this part of the auditory apparatus, concerning which there can be no doubt:

First, it is certain that impressions of sound are received by the terminal filaments of the auditory nerves, and by these nerves are conveyed to the brain.

Second, the functions of the parts composing the external and the middle ear are simply accessory. The sonorous waves are collected by the pavilion and are conveyed by the external meatus to the middle ear; the membrana tympani vibrates under their influence; and they are thus collected, repeated, and transmitted to the internal ear, under the most favorable conditions for producing a proper impression upon the auditory nerves.

In view of these facts, we must look to the functions of semicircular canals and the cochlea, for an elucidation of the problem of the mechanism of the final process of audition; and, in doing this, we come at once to the question of the relative importance of different divisions of the internal ear.

Functions of the Semicircular Canals.—In a memoir presented to the French Academy of Sciences, in 1824, Flourens detailed a number of experiments on pigeons and rabbits, in which he destroyed different portions of the internal ear. In these experiments, the results of which were very distinct, it was shown that destruction of the semicircular canals had apparently no effect upon the sense of hearing, while destruction of the cochlea upon both sides produced

complete deafness.[1] In addition, it was observed that destruction of the semicircular canals on both sides was followed by remarkable disturbances in equilibration. The animals could maintain the standing position, but, as soon as they made any movements, "the head commenced to be agitated; and this agitation increasing with the movements of the body, walking and all regular movements finally became impossible, in nearly the same way as when equilibrium and stability of movements are lost after turning several times or violently shaking the head."[2] These observations of Flourens, at least as far as regards the influence of the semicircular canals upon equilibration, have been confirmed by Goltz, and are sustained by observations on the human subject in the condition known as Ménière's disease.[3] In some more recent experiments, however, Boettcher assumes to have demonstrated that the semicircular canals have nothing to do with equilibration; but all of his observations were made upon frogs, in which deficiency of equilibration and of hearing would be very difficult to determine.[4] As far as we can judge from experimental data, it does not seem probable that the nerves directly concerned in audition are distributed to any considerable extent in the semicircular canals. Indeed, the function of these parts is exceedingly obscure; for we can hardly admit, upon purely anatomical grounds, that they are concerned in the discrimination of the direction of sonorous vibrations, an idea which has been advanced by some physiologists.

Functions of the Parts contained in the Cochlea.—There can be no doubt with regard to the capital point in the physiology of the cochlea; namely, that those branches of the

[1] FLOURENS, *Recherches expérimentales sur les propriétés et les fonctions du système nerveux*, Paris, 1842, p. 443, *et seq.*

[2] *Op. cit.*, p. 446.

[3] See vol. iv., Nervous System, pp. 369, 387.

[4] BOETTCHER, *Kritische Bemerkungen und neue Beiträge zur Literatur des Gehörlabyrinths.—Dorpater medicinische Zeitschrift*, Dorpat, 1872, Bd. iii., S. 108.

auditory nerve which are essential to the sense of hearing and which receive the impressions of sound are distributed mainly in the cochlea. When we come to analyze sonorous impressions, we find that they possess various attributes, such as intensity, quality, and pitch, which have been discussed rather fully under the head of the physics of sound. As far as the terminal filaments of the auditory nerve are concerned, it is evident that the intensity of sound is appreciated in proportion to the power of the impression made upon these nerves, and this point does not demand elaborate discussion. With regard to quality of sound, we have seen that this is due to the form of sonorous vibrations, and that most musical tones are compound, their quality depending largely upon the relative power of the harmonics, partial tones, etc. We have also seen that consonating bodies repeat by influence, not only the actual pitch of tones, but their quality. If there be in the cochlea an anatomical arrangement of rods or fibres by which the sonorous vibrations, conveyed to the ear by the atmosphere, are repeated, there is reason to believe that the quality, as well as the pitch, is reproduced. Narrowing down the question, then, to its most interesting and important point; viz., the appreciation of differences in the pitch of musical tones, we inquire whether there be in the cochlea any arrangement by which the pitch can be repeated. This inquiry can only be answered by a study of the anatomical arrangement of the structures connected with the terminal filaments of the nerves, and the application of physical laws.

The arrangement of the rods which enter into the structure of the organ of Corti has afforded a theoretical explanation of the final mechanism of the appreciation of pitch. Until we come to the internal ear, the action of different portions of the auditory apparatus is simply to conduct and repeat sonorous vibrations; and the sole function of these accessory parts, aside from the protection of the organs, is to convey the vibrations to the terminal nervous filaments.

Whatever be the functions of the membrana tympani in repeating sounds by influence, it is certain that this membrane possesses no true auditory nerves, and that the auditory nerves only are capable of receiving impressions of sound. Thus, hearing, and even the appreciation of pitch, is not necessarily lost after destruction of the membrana tympani; and, if sonorous vibrations reach the auditory nerves, they will be appreciated and appreciated correctly. With this point clearly understood, we are prepared to study the probable functions of the organ of Corti.

When we consider the organ of Corti, with its eight thousand or more rods of different lengths arranged with a certain degree of regularity, a number more than sufficient to represent all the tones of the musical scale, we are not surprised that eminent physiologists regard them as capable of repeating all the shades of tone heard in music. Helmholtz formularizes this idea in the theory that tones conveyed to the cochlea throw into vibration those elements of the organ of Corti which are tuned, so to speak, in unison with them. According to this hypothesis, the rods of Corti constitute a harp of several thousand strings, played upon, as it were, by the sonorous vibrations.[1]

It would be difficult to imagine any thing more beautiful and simple than such an hypothesis as we have just quoted. Attention and education enable persons endowed with what is called a musical ear to discriminate between different tones with great accuracy. Experiments have shown that the situation of the actual appreciation of tones may be restricted to the cochlea; and, in the cochlea, the only anatomical arrangement, as far as we know, which points toward an appreciation of the pitch of different tones is that of the rods of Corti. Still, it must be remembered that the cochlea is so situated as to be removed from the possibility of experimental investigation to prove the theory; and we must carefully study the anatomical arrangement of the parts and the

[1] HELMHOLTZ, *Théorie physiologique de la musique*, Paris, 1868, p. 183, *et seq.*

possible application of physical laws to the supposed vibration of the rods.[1]

Viewing the question from its anatomical aspect, it is by no means certain that the rods of Corti are so attached and stretched that they are capable of separate and individual vibrations. It has not been demonstrated that certain of these rods vibrate under the influence of certain tones, or are tuned in accord with certain tones. Hensen, who has written elaborately upon the very question under consideration, denies the accuracy of the theory of Helmholtz, basing his opinion upon the anatomical arrangement of the rods of Corti, and assumes that it is a physical impossibility for the different rods to vibrate individually, and that it is not cer-

[1] It is a curious historical fact that Du Verney, in a work first published in French, in 1683, and afterward translated into Latin, stated that the filaments of those auditory nerves distributed upon the lamina spiralis were so arranged as to receive the various impressions made by different musical tones. (DU VERNEY, *Tractatus de Organo Auditus*, Lugd. Batav., 1730, pp. 28, 29.) Le Cat, the first edition of whose work on the Senses was published in 1739, also advanced the theory that the cochlea was the only portion of the auditory apparatus capable of appreciating musical tones. After speaking of the vestibule and the semicircular canals as the parts affected by irregular sonorous vibrations, he states that the cochlea has a more delicate function:

"The design of this construction is of the most perfect mechanism. The essential office of an organ of sense is proportionate to its object, and, for the organ of hearing, it is the capacity of being in unison with the different vibrations of the air; these vibrations have infinite differences; their progression is susceptible of infinitely small degrees. An organ, then, is necessary, which is made in unison with all these vibrations, and, in order to receive them distinctly, should be composed of parts, the elasticity of which follows this same progression, insensible, or infinitely small. The spiral in mechanics is the only apparatus adapted to give this insensible gradation."

Farther on, Le Cat states that, "whatever division may be conceived of in tones, there is none which does not meet, in points of this spiral, with its unison, or its equal vibration, thus there is no tone which cannot distinctly impart its vibration to this spiral; and in this consists the grand design of the cochlea. This is why I regard the cochlea as the sanctuary of audition, as the special organ of harmony, or of the most distinct and the most delicate sensation of this kind." (LE CAT, *Traité des sensations*, etc., Paris, 1767, tome ii., pp. 281, 282.) The above is simply the theory of Helmholtz, wanting the exact anatomical and physical details developed by modern researches and experiments.

tain that they are tuned in accord with different tones. Hensen makes, on this point, the following statement:

"It is now my conviction, that by the hypothesis 'more and more corroborated' that the fibres of Corti constitute the organ of the labyrinth tuned to the appreciation of tones, our comprehension and the investigation of the internal ear have taken a false direction.

"I assert, next, that the rods of Corti cannot play the important part in the appreciation of tones, which has been attributed to them in the hypothesis of Helmholtz."[1]

It is pretty evident that, although the theory of Helmholtz is undoubtedly the only one affording any reasonable explanation of the appreciation of tones, it lacks positive anatomical confirmation. And, farthermore, we do not even know the anatomical connections between the rods of Corti and the filaments of the auditory nerves.

In view of the considerations just given, we have simply recited the theory of Du Verney, Le Cat, and Helmholtz, as one which may or may not be sustained hereafter by more exact researches; but at present it must be acknowledged that there is no more satisfactory explanation of the mechanism of the final appreciation of musical tones.

Summary of the Mechanism of Audition.

The waves of sound are simply collected by the pavilion of the ear and are conveyed, through the external meatus, to the membrana tympani. The membrana tympani, a delicate, rounded, concave membrane, receives these waves and is thrown into vibration.

The arrangement of the bones and muscles of the middle ear admits of variations in the tension of the membrana tympani. By increasing the tension of this membrane, the ear may be rendered insensible to grave sounds, while high-

[1] HENSEN, *Experimentelle Studien zur Physiologie des Gehörgans, von* DR. SCHMIDEKAM *mit Zusätzen von* DR. HENSEN.—*Arbeiten aus den Kieler physiologischen Institut*, Kiel, 1869, S. 131.

pitched sounds become more intense; and, in cases of voluntary tension, the limit of perception of high tones may be greatly increased. The membrana tympani obeys the laws of consonance and vibrates strongly under the influence of sounds in unison or in harmony with its fundamental tone, returning, in this way, not only the pitch, but the quality of tones and combinations of tones in harmony. Destruction of the membrane does not necessarily of itself destroy hearing, or even the appreciation of tones, for the impressions may be conducted to the cochlea by the chain of ossicles.

The arrangement of the ossicles and muscles of the middle ear is such that contraction of the tensor tympani renders the articulations firm, tightens the little ligaments, and presses the stapes against the liquid of the labyrinth, so that the chain resembles, in its action, a solid and continuous bony rod. By this arrangement, the sonorous vibrations are conducted to the labyrinth with very little loss of intensity.

The cavity of the tympanum is filled with air, communicates with the mastoid cells, and with the pharynx by means of the Eustachian tube; and, by this means, the pressure of air in its interior is regulated. The labyrinth, consisting of the vestibule, semicircular canals, and cochlea, is filled with liquid, and the different cavities communicate with each other. The vibrations, repeated by the membrana tympani, are conveyed by the chain of bones to the liquid of the labyrinth, and by it to the terminal filaments of the auditory nerves.

The vestibule and semicircular canals seem to possess much less importance in the appreciation of sound than the cochlea. In the cochlea, throughout the entire extent of the spiral canal, is the organ of Corti, presenting, among other structures, about 8,700 rods, varying in length, called the rods of Corti. But little is known of the anatomical relations between the auditory nerves and the organ of Corti; still, it is thought, as a matter of pure theory, that the rods of Corti are tuned in unison with different tones, that they

repeat the tones conveyed to the cochlea, and that we are thus enabled to distinguish the different tones in music.

We have no very definite knowledge of the functions of the cells of the organ of Corti, of the otoliths, and of various other structures in the auditory apparatus. Sounds may be conducted to the auditory nerves through the bones of the head and the Eustachian tube, as is shown by the simple and familiar experiment of placing a tuning-fork in vibration in contact with the head or between the teeth.

CHAPTER X.

GUSTATION.

Savory substances—Relations between gustation and olfaction; taste and flavor—Modifications of the sense of taste—Nerves of taste—Chorda tympani—Facial paralysis with impairment of taste—Paralysis of general sensibility of the tongue without impairment of taste—Glosso-pharyngeal nerve (first division of the eighth)—Physiological anatomy—General properties of the glosso-pharyngeal—Relations of the glosso-pharyngeal nerves to gustation—Differences in the properties of different portions of the gustatory organ—Mechanism of gustation—Physiological anatomy of the organ of taste—Papillæ of the tongue—Taste-buds, or taste-beakers—Connections of the nerves with the organs of taste.

THE special sense of taste enables us to appreciate what is known as the savor of certain substances introduced into the mouth; and this sense exists, in general terms, in parts supplied by filaments from the lingual branch of the fifth and the glosso-pharyngeal nerves.

It is somewhat difficult to define precisely what is meant by savory substances. The word savory is frequently used so as to include the quality of odor; and, indeed, the senses of gustation and olfaction are quite closely connected. Almost all substances that affect the sense of taste possess a certain odor, and taste and smell are thus simultaneously impressed. Medicinal articles of a disagreeable taste may sometimes be swallowed without making a very disagreeable impression, if the nares be closed. Again, when the nares are closed or when the sense of smell is rendered obtuse by an affection of the Schneiderian membrane, it is difficult to distinguish delicate shades of flavor, as the differences in wines. This is a matter of common observation and remark. There

are, also, certain articles which have a repulsive odor, the taste of which is not disagreeable, such as some varieties of old cheese. As a rule, however, articles agreeable to the taste possess an agreeable odor, and the senses of taste and smell are not easily separated from each other. These facts have led to a distinction, which cannot, however, be always made with accuracy, between true tastes and flavors. It is assumed, by some physiologists, that the true tastes are quite simple, presenting the qualities which we recognize as sweet, acid, saline, and bitter; while the more delicate shades of what are called flavors nearly always involve olfactory impressions, which it is difficult to separate entirely from gustation. We have already incidentally alluded to this point in treating of olfaction, and have cited cases of loss of the sense of smell with no impairment of what we have just described as true taste, but a loss of power of appreciating flavors.[1]

If we apply the term savor exclusively to the quality which makes an impression upon the sense of taste, we recognize that the sensation is special in its character, and different from the tactile sensibility of the parts involved and from the sensation of temperature. The terminal filaments of the gustatory nerves are impressed by the actual contact of savory substances, which must, of necessity, be soluble. To a certain extent, there is a natural classification of savors, some of which are agreeable, and others disagreeable; but even this distinction is modified by habit, education, and various other circumstances. Articles that are unpleasant in early life often become agreeable in later years. Inasmuch as the taste is, to some extent, an expression of the nutritive demands of the system, it is found to vary, under different conditions. Chlorotic females, for example, frequently crave the most unnatural articles, and these morbid tastes may disappear under appropriate treatment. Inhabitants of the frigid zones seem to crave fatty articles, and will even drink rancid oils with avidity. Patients often become accustomed

[1] See page 35.

to the most disagreeable remedies and take them without repugnance. Again, the most savory dishes may even excite disgust, when the sense of taste has become cloyed, while abstinence sometimes lends a delicious flavor to the simplest articles of food. The taste for certain articles is certainly acquired, and this is almost always true of tobacco, now so largely used in civilized countries.

Any thing more than the simplest classification of savors is difficult, if not impossible. We recognize that certain articles are bitter or sweet, empyreumatic or insipid, acid or alkaline, etc., but, beyond these simple distinctions, the shades of distinction are closely connected with olfaction and are too delicate and numerous for detailed description. Many persons are comparatively insensible to nice distinctions of taste, while others recognize with facility the most delicate differences. Strong impressions may remove, for a time, the appreciation of less powerful and decided flavors. The tempting of the appetite by a proper gradation of gustatory and odorous impressions is illustrated in the modern *cuisine*, which aims at an artistic combination and succession of dishes and wines, so that the agreeable sensations are prolonged to the utmost limit. This may often be regarded as a violation of strictly hygienic principles, but it none the less exemplifies the cultivation of the sense of taste.

In discussing the physiology of taste, we shall avoid an elaborate and artificial classification of savory articles, and use the terms sweet, acid, bitter, etc., as they are commonly understood. We shall first describe the physiological anatomy and properties of the gustatory nerves, and then consider the mechanism of gustation, the special organs of taste, and the probable mode of connection between the organs of taste and the nerves.

Nerves of Taste.—Two nerves, the chorda tympani and the glosso-pharyngeal, preside over the sense of taste. These nerves seem to be distributed to distinct portions of the gus-

tatory apparatus and to have somewhat different functions. The chorda tympani has already been referred to as one of the branches of the facial;[1] the glosso-pharyngeal, one of the nerves of the eighth pair, has not yet been described.

Chorda Tympani.—In the description we have given of the facial, the chorda tympani is spoken of as the fourth branch. It passes through the tympanum, between the ossicles of the ear, and joins the inferior maxillary division of the fifth, at an acute angle, between the two pterygoid muscles, becoming so closely united with it that it cannot be followed farther by ordinary dissection. It is impossible to determine with certainty from what root the filaments of this branch derive their origin, whether from the main trunk or the intermediary nerve of Wrisberg; but experiments have shown that it possesses functions entirely distinct from those of the other branches of the facial. The lingual branch of the inferior maxillary division of the fifth has been called the gustatory branch; but this is an error; for, as we shall see, the fifth has nothing to do with gustation, except that it is joined with filaments of the chorda tympani, which reach the tongue through the lingual branch.

As regards the course of the filaments of the chorda tympani after this nerve has joined the fifth, there can be no doubt, both from the effect upon taste following its division,[2] and the alteration of the nerve-fibres. Vulpian and Prevost,[3] by the so-called Wallerian method, after dividing the chorda tympani, found degenerated fibres at the terminations of the lingual branch of the fifth in the mucous membrane of the tongue, the fibres being examined ten days or more after the section. It is well known that, a number of days after the section of a nerve, its fibres of distribution undergo change,

[1] See vol. iv., Nervous System, p. 149, *et seq.*

[2] Vulpian, *Études sur l'appareil vaso-moteur.—Revue scientifique*, Paris, 1873, 2e série, tome iii., p. 179.

[3] Prevost, *Nouvelles expériences relatives aux fonctions gustatives du nerf lingual.—Archives de physiologie*, Paris, 1873, tome v., p. 388.

and these observations leave no doubt of the fact that the chorda tympani is really distributed to the lingual mucous membrane. Observations on the sense of taste show that the chorda tympani is distributed to about the anterior two-thirds of the tongue.

The general properties of the chorda tympani have only been ascertained by observations made after its paralysis or division. All experiments, in which excitation has been applied directly to the nerve in living animals, have been negative in their results. Longet states that, when the nerve has been isolated as completely as possible, and all reflex action is excluded, its galvanization produces no movement in the tongue.[1]

For a long time, the lingual branch of the inferior maxillary division of the fifth has been regarded as a nerve of taste, and has been called the gustatory branch. In 1786, Caldani noted, in an affection of the fifth pair, called "cynic spasm," loss of the sense of taste.[2] In 1818, Bellingeri discussed the question whether the sense of taste in the tongue was derived from proper filaments of the fifth pair or from filaments passing to the fifth from the seventh by the chorda tympani, and came to the conclusion that the gustatory sense was due to the filaments of the chorda tympani.[3] In 1821, Professor Roux described his own case of paralysis of the facial, and noted that "the sense of taste was affected in the right side of the tongue, so that every thing tasted metallic;[4] but, in this observation, no mention was made of the chorda tympani. In 1831, Montault noted loss of taste in deep palsy of the facial and explained it by indicating an affection of the chorda tympani.[5] Since that time, it has been established

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 581, note.

[2] CALDANI, *Institutiones Physiologicæ*, Venetiis, 1786, p. 168.

[3] BELLINGERI, *Dissertatio Inauguralis, Quinti, et Septimi Paris Functiones*, 1818, p. 170.

[4] BELL, *The Nervous System of the Human Body*, London, 1844, p. 329.

[5] MONTAULT, *Dissertation sur l'hémiplégie faciale*, *Thèse*, No. 300, Paris, 1831, p. 22.

beyond question that, in cases of facial palsy in which the lesion affects the root so deeply as to involve the chorda tympani, there is loss of taste in the anterior two-thirds of the tongue, tactile sensibility being unaffected. Cases illustrating this fact have been cited by Stich,[1] Bernard,[2] Lusanna,[3] Bazire,[4] and many others. In another volume, we have given the report of a case of facial paralysis produced by a gunshot-wound through the head, in which we observed that the sense of taste was entirely abolished in the anterior portion of the tongue on the affected side.[5]

Aside from cases of paralysis of the facial with impairment of taste, in which the general sensibility of the tongue is intact, numerous instances are on record of affections of the fifth pair, in which the tongue is absolutely insensible to ordinary impressions, the sense of taste being preserved. A number of such cases have been reported by Schiff,[6] Lusanna,[7] and others; and show conclusively that the fifth pair presides over general sensibility only, and that it is not a gustatory nerve, except by virtue of filaments derived from the chorda tympani.

Passing from the consideration of pathological cases to experiments upon living animals, the results are equally satisfactory. Although it is somewhat difficult to observe im-

[1] STICH, *Beiträge zur Kenntniss der Chorda tympani.—Annalen des Charité-Krankenhauses, etc., zu Berlin*, Berlin, 1857, Bd. viii., S. 59, *et seq.*

[2] BERNARD, *Leçons sur la physiologie et la pathologie du système nerveux*, Paris, 1858, tome ii., p. 120, *et seq.*

[3] LUSANNA, *Recherches expérimentales et observations pathologiques sur les nerfs du gout.—Archives de physiologie*, Paris, 1869, tome ii., p. 20, *et seq.*

[4] BAZIRE, *Case of Facial Paralysis, with Impairment of Taste and Acoustic Hyperæsthesia on the same side as the Paralysis.—Quarterly Journal of Psychological Medicine*, New York, 1868, vol. ii., p. 186.

[5] See vol. iv., Nervous System, p. 157, where we have given full details of this case.

[6] SCHIFF, *Leçons sur la physiologie de la digestion*, Florence et Turin, 1867, tome i., p. 103, *et seq.*

[7] LUSANNA, *Sur les nerfs du goût.—Archives de physiologie*, Paris, 1871–'72, tome iv., p. 151, *et seq.*

pairment of taste in animals, Bernard and others have succeeded in training dogs and cats so as to observe the effects of colocynth and various sapid substances applied to the tongue. In a great number of experiments of this kind, made by Bernard,[1] Schiff,[2] and Lusanna,[3] it has been observed that, after section of the chorda tympani, or of the facial so as to involve the chorda tympani, the sense of taste is abolished in the anterior two-thirds of the tongue on the side of the section. However this result may be explained, the fact remains, that section of the nerve in the lower animals is followed by the same results as those observed in pathological observations. In a remarkable case reported by Moos,[4] the introduction of an artificial membrana tympani was followed by loss of taste upon the corresponding side of the tongue, and upon both sides, when a membrane was introduced into each ear. This disappeared when the membranes were removed, and the phenomena were referred to pressure upon the chorda tympani. Experimenters are somewhat at variance with regard to the effects observed upon animals, some asserting that the sensations of taste are simply delayed in their manifestation; but we must remember the difficulty of such observations, and we are to rely mainly upon the unmis-

[1] BERNARD, *Système nerveux*, Paris, 1858, tome ii., p. 122.

[2] SCHIFF, *Digestion*, Florence et Turin, 1867, tome i., p. 183.

[3] LUSANNA, *Recherches expérimentales et observations pathologiques sur les nerfs du gout.—Archives de physiologie*, Paris, 1869, tome ii., p. 201.

In some of the experiments referred to, it is stated that the gustatory impression is retarded and not entirely destroyed. This is explained on the supposition that section of the nerve renders the mucous membrane dry, and that the action of sapid substances is thereby delayed; but it is equally reasonable to suppose that, after a time, the articles are diffused and impress branches of the glosso-pharyngeal.

[4] MOOS, *Alterations of Taste and Sensibility in the Tongue by the Application of an Artificial Tympanum in a Case of Large Perforations in both Membranæ Tympani.—Archives of Ophthalmology and Otology*, New York, 1869, vol. i., p. 140, *et seq.*

The symptoms in this case are rather indefinitely described by the patient, and no very accurate observations were made. The patient also noted some interference with the general sensibility of the tongue.

takable phenomena noted in cases of affection of the chorda tympani in the human subject.

It seems tolerably certain, first, that the gustatory filaments of the lingual branch of the fifth are derived exclusively from the chorda tympani; second, that the chorda tympani, viewed as a gustatory nerve, is really a branch of the facial; third, that many cases of paralysis of the entire large root of the fifth, in the human subject, present loss of general sensibility in the tongue and no alteration of taste; and fourth, that paralysis of the facial, behind the origin of the chorda tympani, is attended with loss of taste in the anterior two-thirds of the tongue, without any affection of the general sensibility of this organ.

We have made the above statement with all the necessary qualifications, and with an appreciation of the value of the various experiments bearing upon the question. It is fair to say that section of the fifth at or near the ganglion of Gasser is said to abolish the sense of taste in the anterior portion of the tongue, as well as the general sensibility; but it must be remembered that it is difficult to make observations on the sense of taste in the lower animals, especially after paralysis of sensation in the tongue; and that numerous cases are on record, to which we have already referred, in which, in the human subject, general sensibility in the tongue was absent, the sense of taste remaining. On the other hand, in certain cases of paralysis of the facial, the sense of taste is absent, while general sensibility is intact. In view of this fact, we cannot admit the proposition of Schiff, that the gustatory nerves of the anterior portion of the tongue emerge from the encephalon with the roots of the fifth.[1] As regards the mechanism of the action of the chorda tympani in gustation, we cannot adopt the view of Bernard,[2] that it acts as a

[1] SCHIFF, *Leçons sur la physiologie de la digestion*, Florence et Turin, 1867, tome i., p. 140; and, *Neue Untersuchungen über die Geschmaksnerven des vorderen Theiles der Zunge.—Untersuchungen zur Naturlehre*, etc., Giessen, 1870, Bd. x., S. 406, *et seq.*

[2] BERNARD, *Système nerveux*, Paris, 1858, tome ii., p. 111.

motor nerve—probably through the salivary glands—in moistening the gustatory membrane.

As we have already remarked, it is difficult to determine the exact origin of the filaments of the chorda tympani. They may come from the root called the nerve of Wrisberg, but this has not been positively established, either anatomically or physiologically; but the course of the nerve, after it has joined the lingual branch of the fifth, is sufficiently clear, as we have seen. Schiff, who supposes that the filaments presiding over the sense of taste are derived originally from the fifth, assumes that these filaments "emerge from the cranium with the second branch of this nerve, enter the spheno-palatine ganglion," and then pass to the third branch by a course which is as yet undetermined.[1] If this be the fact, and the idea is based chiefly upon physiological grounds, extirpation of the spheno-palatine ganglia should abolish the sense of taste in the anterior portion of the tongue. Although the operation of removal of both these ganglia is difficult, this has been done successfully by Prevost, who denies that such a mutilation has any effect upon gustation.[2]

As a summary of our knowledge regarding the gustatory properties of the anterior two-thirds of the tongue, certainly in the human subject, it may be stated without reserve, that these properties depend upon the chorda tympani, its gustatory filaments being derived from the facial, and taking their course to the tongue with the lingual branch of the inferior maxillary division of the fifth. In addition, the lingual branch of the fifth contains filaments, derived from the large root of this nerve, which endow the mucous membrane with general sensibility.

Glosso-Pharyngeal (First Division of the Eighth).—The glosso-pharyngeal is distributed to those portions of the gus-

[1] SCHIFF, *Digestion*, Florence et Turin, 1867, tome i., p. 140.

[2] PREVOST, *Nouvelles expériences relatives aux fonctions gustatives du nerf lingual.—Archives de physiologie*, Paris, 1878, tome v., p. 387.

tatory mucous membrane not supplied by filaments from the chorda tympani. It is undoubtedly a nerve of taste; and the question of its other functions will be fully considered in connection with its general properties, as well as the differences between this nerve and the chorda tympani. We have mentioned this nerve in another volume as the first division of the eighth pair, according to the classification of Willis, but have to treat of its physiological anatomy in this connection, as its most important function is in connection with gustation.

Physiological Anatomy.—The apparent origin of the glosso-pharyngeal is from the groove between the lateral tracts of the medulla oblongata and the inferior peduncle of the cerebellum, between the roots of the auditory nerve above and the pneumogastric below. A number of its filaments of origin come from the medulla and a portion from the peduncle. The deep origin is nearly the same as that of the pneumogastric, its filaments arising primarily from the gray substance of the medulla oblongata.[1] From this origin, the filaments pass forward and outward to the posterior foramen lacerum, which the nerve enters in company with the pneumogastric, the spinal accessory, and the internal jugular vein. At the upper portion of the foramen, is a small ganglion, the jugular ganglion, including only a portion of the root. Within the foramen, is the main ganglion, including all of the filaments of the trunk, called the petrous ganglion, or the ganglion of Andersch, after the anatomist by whom it was first described.[2]

At or near the ganglion of Andersch, the nerve usually receives a delicate filament from the pneumogastric. This communication is sometimes wanting. The same may be said of a small filament passing to the glosso-pharyngeal from

[1] See vol. iv., Nervous System, p. 204.

[2] ANDERSCH, *Fragmentum Descriptionis Nervorum Cardiacorum;* in LUDWIG, *Scriptores Nevrologici minores selecti*, Lipsiæ, 1792, tomus ii., p. 115.

the facial, which is not constant. Branches from the glosso-pharyngeal go to the otic ganglion and to the carotid plexus of the sympathetic.

The distribution of the glosso-pharyngeal is quite extensive. The tympanic branch, the nerve of Jacobson, arises from the anterior and external part of the ganglion of Andersch, and enters the cavity of the tympanum, where it divides into six branches. Of these six branches, two posterior are distributed to the mucous membrane of the fenestra rotunda and the membrane surrounding the fenestra ovalis; two anterior are distributed, one to the carotid canal, where it anastomoses with a branch from the superior cervical ganglion, and the other to the mucous membrane of the Eustachian tube; two superior branches are distributed to the otic ganglion and, as is stated by some anatomists, to the spheno-palatine ganglion.[1]

A little below the posterior foramen lacerum, the glosso-pharyngeal sends branches to the posterior belly of the digastric and to the stylo-hyoid muscle. There is also a branch which joins a filament from the facial to the stylo-glossus.

Opposite the middle constrictor of the pharynx, three or four branches join branches from the pneumogastric and the sympathetic to form together the pharyngeal plexus. This plexus contains numerous ganglionic points, and filaments of distribution from the three nerves go to the mucous membrane and the constrictors of the pharynx. Probably, the mucous membrane is supplied by the glosso-pharyngeal. As we have stated in another volume, it is probable that the muscles of the pharynx are supplied by filaments from the pneumogastric, which are originally derived from the spinal accessory.[2]

Near the base of the tongue, branches are sent to the mucous membrane covering the tonsils and the soft palate.

The lingual branches penetrate the tongue about midway

[1] Sappey, *Traité d'anatomie*, Paris, 1871, tome iii., p. 339.

[2] See vol. iv., Nervous System, p. 207

between its border and centre, and are distributed to the mucous membrane at its base, being probably connected with the papillæ.

General Properties of the Glosso-Pharyngeal.—As in the case of other sensory nerves emerging from the cranial cavity, it is important, in studying the general properties of the glosso-pharyngeal, to make our observations under certain conditions. First, it must be remembered that this nerve contracts anastomoses a short distance from its origin. As we desire to know the properties of the original filaments of the nerve, we must operate upon it before it has received communicating fibres. Next, in irritating sensory nerves, we are liable to produce reflex contractions. To avoid this, the nerve must be divided; when the reflex contractions will only follow stimulation of the central end. It is probably from a neglect of these essential experimental conditions, that the results of direct observation have been so discordant in the hands of different physiologists.

To begin with, we shall assume that the glosso-pharyngeal must be irritated between its origin and the ganglion of Andersch, in order to avoid anastomosing filaments from motor nerves, and that the nerve must be divided, and irritation be applied to its peripheral end, to avoid reflex movements. Assuming these conditions as essential, we can discard most of the earlier experiments, as open to the objections we have mentioned. Longet, operating on horses and dogs, after removal of the cerebral lobes and division of the glosso-pharyngeal, found that galvanization of the peripheral extremity of the nerve did not produce movements of the palate or pharynx;[1] and, from these experiments, he concludes that the nerves are exclusively sensory at their roots, or, at least, that they do not contain motor filaments. This we accept as conclusive, notwithstanding the contrary assertion of Chauveau,

[1] LONGET, *Anatomie et physiologie du système nerveux*, Paris, 1842, tome ii., p. 220; and, *Traité de physiologie*, Paris, 1869, tome iii., p. 501.

who operated without dividing the nerves, and who observed contractions, which were undoubtedly reflex.[1] In another volume, under the head of movements of the palate and uvula, we have cited in detail a series of experiments by Bernard and Davaine, which illustrate the reflex movements of the velum palati through the facial, produced by galvanization of the glosso-pharyngeal.[2] As a complement to the first experiments of Longet, just cited, the same observer noted contractions of the pharyngeal muscles following galvanization of the peripheral end of the divided nerve in the neck, which could only be produced by the action of motor anastomosing filaments.[3]

As regards general sensibility, there can be no doubt of the fact that the glosso-pharyngeal is sensory, though its sensibility is somewhat obtuse. In the experiments in which the nerve has seemed to be insensible to ordinary impressions, it is probable that the animals operated upon had been exhausted more or less by pain and loss of blood in the operation of exposing the nerve, which, it is well known, abolish the sensibility of some of the nerves. Longet states distinctly that, unless the animals (dogs) be already exhausted by resistance during the operation, they have always appeared to suffer pain on pinching or dividing the glosso-pharyngeal.[4] The observations of Schiff, also, lead to a similar conclusion.[5]

Experiments upon the glosso-pharyngeal are not very definite and satisfactory in their results, as regards the general sensibility of the base of the tongue, palate, and pharynx. The sensibility of these parts seems to depend chiefly upon branches of the fifth, passing to the mucous membrane through Meckel's ganglion. Experiments show, also, that the

[1] CHAUVEAU, *Du nerf pneumogastrique.—Journal de la physiologie*, Paris, 1862, tome v., p. 209.

[2] See vol. iv., Nervous System, p. 161.

[3] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 503.

[4] *Op. cit.*, p. 503.

[5] SCHIFF, *Leçons sur la physiologie de la digestion*, Florence et Turin, 1867 p. 93.

reflex phenomena of deglutition take place mainly through these branches of the fifth,[1] and that the glosso-pharyngeal has little or nothing to do with the process. In fact, after division of both glosso-pharyngeal nerves, deglutition does not seem to be affected.[2]

With these remarks, we dismiss the functions of the glosso-pharyngeals as nerves of general sensibility, and shall consider, in detail, their relations to the sense of taste.

Relations of the Glosso-Pharyngeal Nerves to Gustation.—Physiological writers quote the observations of Panizza, as showing that these nerves preside over the sense of taste. Panizza, however, appears to have been in error in supposing that the nerves under consideration have no influence over general sensibility, and that their section abolishes taste completely.[3] That this exclusive view is erroneous, is sufficiently well shown by observations upon the gustatory functions of the chorda tympani. The observations of Panizza appeared in 1834; and, in 1839, Valentin published a number of experiments, in which the views of Panizza were apparently confirmed, and he also asserted that taste was abolished by section of both glosso-pharyngeals in dogs.[4] There can be no doubt, from these and other experiments, that the glosso-pharyngeals are nerves of taste and are distributed to the base of the tongue; and it is probable that those who have denied this property have mistaken for the glosso-pharyngeals the pharyngeal branches of the spinal accessory.[5]

In the experiments both of Panizza and Valentin, after

[1] See vol. iv., Nervous System, pp. 195, 217.

[2] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 507.

WALLER ET PREVOST, *Étude relative aux nerfs sensitifs que président aux phénomènes réflexes de la déglutition.—Archives de physiologie*, Paris, 1870, tome iii., p. 353.

[3] LONGET, *op. cit.*, p. 504.

LUSANNA, *Archives de physiologie*, Paris, 1869, tome ii., p. 21.

[4] VALENTIN, *De Functionibus Nervorum Cerebralium et Nervi Sympathici*, Bernæ, 1839, p. 41.

[5] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 504.

section of the nerves on both sides, animals ate, without repugnance, meat mixed with colocynth, and drank colocynth mixed with milk, while other animals refused these articles with every indication of disgust. This fact has also been observed by Longet[1] and by Lusanna.[2]

Relying upon experiments on the inferior animals, particularly dogs, it seems pretty certain that there are two nerves presiding over the sense of taste: The chorda tympani gives this sense to the anterior portion of the tongue exclusively, probably the anterior two-thirds; the glosso-pharyngeal supplies this sense to the posterior portion of the tongue; the chorda tympani seems to have nothing to do with general sensibility; while the glosso-pharyngeal is an ordinary sensory nerve, as well as a nerve of special sense.

To conclude this portion of our subject, we may cite quite an elaborate series of observations by Lusanna, showing that the sense of taste varies in different portions of the gustatory apparatus.[3]

Where there are such differences in the delicacy of the

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 505.

[2] LUSANNA, *Archives de physiologie*, Paris, 1869, tome ii., p. 24.

[3] LUSANNA, *Recherches expérimentales et observations pathologiques sur les nerfs du gout.—Archives de physiologie*, Paris, 1869, tome ii., p. 208. The observations in the table were made by the pupils of Lusanna, under his direction.

" A. Savors equally well appreciated at the anterior and posterior part of the tongue.

1. Aliments.	*a.*	Taste of milk.
	b.	" meats.
	c.	" farinaceous substances.
	d.	" saccharine substances.
	e.	" fatty substances.
	f.	" alcohol.
	g.	" wines.
	h.	" acids.
	i.	" salts.
2. Seasonings, aromas, coffee, pepper, absinthe, essential oils.	*a.*	Piquant taste.
	b.	Aromatic "
	c.	Pungent "
	d.	Ethereal "

" B. Savors that are slightly or not at all appreciated at the anterior portion

sense of taste as exist usually in different individuals, it must be difficult to describe with accuracy delicate shades of savor, particularly in alimentary substances; but the distinct impressions of acidity or bitter quality are easily recognizable. From the observations just cited, it would appear that saline, acid, and styptic tastes are best appreciated through the chorda tympani, and that sweet, alkaline, bitter, and metallic impressions are received mainly by the glosso-pharyngeal.

Mechanism of Gustation.—The mode in which sapid substances are brought in contact with the organ of taste is so simple, that we need only allude to it, before we study the anatomy of the parts directly concerned, and their connections with the terminal filaments of the gustatory nerves. In the first place, the articles which make the special impression are in solution; introduced into the mouth, they increase

of the tongue, but which are appreciated, to a high degree, at its posterior portion.

a. Caustic and acid (mineral acids, etc.).
b. Metallic (sulphate of iron, alum, etc.).
c. Alkaline.
d. Ammoniacal, urinous.
e. Acrid (jalap, worm-seed, onions, garlics, etc.).
f. Bitter (colocynth, quinine, aloes).
g. Putrid.

"C. Savors appreciated in one way by the chorda tympani, and in another by the glosso-pharyngeal.

Different Articles.	At the anterior part of the tongue.	At the posterior part of the tongue.
a. Chloride of potassium.	Taste, cool, salt.	Sweetish.
b. Acetate of potash.	" burning, acid, piquant.	Bitter, nauseous, neither acrid nor piquant.
c. Nitrate of potash.	" cool, piquant.	Bitter, insipid.
d. Alum.	" acid, cool, styptic.	Sweetish, not acid.
e. Sulphate of soda.	" salt.	Bitter.
f. Acetate of lead.	" cool, piquant, styptic.	Saccharine.
g. Oxalic acid.	" piquant.	Bitter.
h. Bisulphate of quinine.	" piquant, acid, cool.	Very bitter."

the flow of saliva, the reflex action involving chiefly the submaxillary and sublingual glands; there is usually more or less mastication, which increases the flow of the parotid saliva; and, during the acts of mastication and the first stages of deglutition, the sapid substances are distributed over the gustatory membrane, so much so, indeed, that it is difficult to exactly locate the seat of the special impression. In this way, by the movements of the tongue, aided by an increased flow of saliva, the actual contact of the savory articles is rapidly effected. The thorough distribution of these substances over the tongue and the mucous membrane of the general buccal cavity leads to a certain amount of confusion in our appreciation of the special impressions; and, in order to ascertain if different portions of the membrane possess different properties, it is necessary to make careful experiments, limiting the points of contact as closely as possible. This has been done, with the result of showing that the true gustatory organ is quite restricted in its extent, and, as such, it demands special anatomical description.

Physiological Anatomy of the Organ of Taste.—Recent anatomical and physiological researches have shown that, at least in the human subject, the organ of taste is probably confined to the dorsal surface of the tongue. In the old experiments of Vernière and of Guyot and Admyrauld, quoted and in part confirmed by Longet,[1] the gustatory sensibility of the tongue was established; and Longet, from observations on his own person, touching different parts of the mucous membrane with a sponge soaked in sapid solutions, came to the following conclusions: "1. I cannot admit gustatory sensibility in the mucous membrane which covers the superior portion of the velum palati, nor for that which covers the sublingual glands and the inferior surface of the tongue. 2. I do not regard the superior and middle portion of the tongue as absolutely devoid of this kind of sensibility."

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 55.

When we examine the structure of the mucous membrane of the mouth, tongue, and palate, we find that the upper surface of the tongue presents numerous papillæ, called, in contradistinction to the filiform papillæ, fungiform and circumvallate. These are not found on its under surface, nor anywhere except on the superior surface. It is pretty well established, particularly since the recent very elaborate observations of Dr. Camerer, of Württemberg, that the circumvallate and fungiform papillæ alone are the organs of taste. This experimenter, by the application of solutions to different parts through fine glass tubes, concluded that the parts around a papilla have no gustatory sensibility, but that different savors can be distinguished when a single papilla is touched.[1] These observations give a new importance to the peculiar papillæ of the tongue, and we therefore present a description of their arrangement and structure.

In Fig. 20, which represents the dorsal surface of the tongue, the large, circumvallate papillæ, which usually number from seven to twelve, are seen in the form of a V, occupying the base of the tongue. The fungiform papillæ are scattered over the surface, but are most numerous at the point and near the borders. Both of these varieties of papillæ are distinguishable by the naked eye.

The circumvallate papillæ are simply enlarged fungiform papillæ, each one surrounded by a circular ridge, or wall, and covered by numerous small, secondary papillæ. The fungiform papillæ have a short, thick pedicle and enlarged, rounded extremities. According to Sappey, from one hundred and fifty to two hundred of these can easily be counted.[2] They, also, present secondary papillæ on their surface. When the mucous membrane of the tongue is examined with a low magnifying power, particularly after maceration in acetic or

[1] Camerer, *Ueber die Abhängigkeit des Geschmacksinns von der gereizten Stelle der Mundhöhle.—Zeitschrift für Biologie*, München, 1870, Bd. vi., S. 440.

[2] Sappey, *Traité d'anatomie*, Paris, 1871, tome iii., p. 618.

dilute hydrochloric acid, their structure is readily observed. They are abundantly supplied with blood-vessels and nerves.

Fig. 26.

1, 1, circumvallate papillæ; 2, median circumvallate papilla, which entirely fills the foramen cæcum; 3, 3, 3, 3, fungiform papillæ; 4, 4, filiform papillæ; 5, 5, vertical folds and furrows of the border of the tongue; 6, 6, 6, 6, glands at the base of the tongue; 7, 7, tonsils; 8, epiglottis; 9, median glosso-epiglottic fold. (SAPPEY, *Traité d'anatomie*, Paris, 1871, tome iii., p. 617.)

Taste-Buds, or Taste-Beakers.—A few years ago, Lovén

and, a little later, Schwalbe[1] described, under these names, peculiar structures, which are supposed to be the true organs of taste. They are found on the lateral slopes of the circumvallate papillæ and occasionally on the fungiform papillæ. The structure of these organs is very simple. They consist of flask-like collections of spindle-shaped cells, which are received into little excavations in the epithelial covering of the mucous membrane, the bottom resting upon the con-

FIG. 21. FIG. 22.

Fig. 21. Medium-sized circumvallate papilla.—1, papilla, the base only being apparent: it is seen that the base is covered with secondary papillæ; 2, groove between the papilla and the surrounding wall; 3, 3, wall of the papilla.

Fig. 22. Fungiform, filiform, and hemispherical papillæ.—1, 1, two fungiform papillæ, covered with secondary papillæ; 2, 2, 2, filiform papillæ; 3, a filiform papilla, the prolongations of which are turned outward; 4, a filiform papilla, with vertical prolongations; 5, 5, small filiform papillæ, with the prolongations turned inward; 6, 6, filiform papillæ with striations at their bases; 7, 7, hemispherical papillæ, slightly apparent, situated between the fungiform and the filiform papillæ. (SAPPEY, *Traité d'anatomie*, Paris, 1871, tome iii., p. 619.)

nective-tissue layer. Their form is ovoid, and, at the neck of the flask, is a rounded opening, called the taste-pore. Their length is from $\frac{1}{310}$ to $\frac{1}{300}$, and their transverse diameter, about $\frac{1}{300}$ of an inch.[2] The cavity of the taste-beakers is

[1] SCHWALBE, *Ueber die Geschmacksorgane der Säugethiere und des Menschen.*—*Archiv für mikroskopische Anatomie*, Bonn, 1868, Bd. iv., S. 154.

In the same *Archiv*, 1872, Bd. viii., S. 660, is a note by Max Schultze, stating that the discovery of the *Schmeckbecher* had been anticipated in a Swedish publication, by Lovén.

[2] ENGELMANN, in STRICKER, *Manual of Human and Comparative Histology*, The New Sydenham Society, London, 1873, vol. iii., p. 2.

filled with cells, of which two kinds are described. The first variety, the outer cells, or the cover-cells, are spindle-shaped, and curved, to correspond to the wall of the beaker. These come to a point at the taste-pore. In the interior of the beaker, are elongated cells, with large, clear nuclei, which are

FIG. 98.

Taste-buds from the lateral taste-organ of the rabbit. (ENGELMANN, in STRICKER, *Handbuch der Lehre von den Geweben*, Leipzig, 1868, S. 828.)

called taste-cells. It is supposed that nerve-fibrils are connected directly with these cells.[1] As far as we can learn, the only reason why these structures are connected with the physiology of gustation is on account of their anatomical relations to the gustatory papillæ.

It now only remains to note the ultimate distribution of the nerves in the gustatory organ. Upon this point, anatomical researches are not entirely satisfactory. However, the following description, by Elin, may be regarded as probably correct, though the facts have not been absolutely demonstrated. According to this authority, from the submucous tissue, small nerve-branches pass perpendicularly to the upper layer of the membrane. These fibres have a varicose appearance. In the most superficial layer of the mucous membrane, there is a net-work of fine, non-medullated fibres;

[1] ENGELMANN, in STRICKER, *Manual of Human and Comparative Histology*, The New Sydenham Society, London, 1873, vol. iii., p. 9.

from this net-work, branches follow the blood-vessels into the papillæ and penetrate the epithelium. Sometimes, though more seldom, they pass into the epithelium lying between the papillæ. In this layer, there are branches which end, some in nerve-cells, and some taking a winding course and passing into neighboring fibres.[1] These descriptions are from preparations made with chloride of gold; but the plates by which they are illustrated are somewhat unsatisfactory.

According to the views of those who have described the so-called taste-beakers, sapid solutions find their way into the interior of these structures through the taste-pores, come in contact with what have been called the taste-cells, these structures being directly connected with the terminal filaments of the gustatory nerves.

[1] ELIN, *Zur Kentniss der feineren Nerven der Mundhöhlenschleimhaut — Archiv für mikroscopische Anatomie*, Bonn, 1871, Bd. vii., S. 387.

CHAPTER XI.

GENERATION—FEMALE ORGANS.

General considerations—Sexual generation—Spontaneous generation, so called—Female organs of generation—General arrangement of the female organs—External and internal organs—The ovaries—Graafian follicles—Primordial ova—Erectile tissue of the ovaries—Development of the Graafian follicles—The parovarium—The uterus—Muscular tissue of the uterus—Mucous membrane of the uterus—Uterine tubes—Blood-vessels and erectile tissue of the uterus—The Fallopian tubes.

A REVIEW of the physiological processes which we have thus far studied shows that the functions of the perfected organism are divided into two great classes:

The first class of functions may be grouped under the general head of nutrition, taken in its widest sense. Nutrition is common to animal and vegetable life; and this is sometimes called a vegetative process.

The study of nutrition involves the following considerations: First, the blood, which is the great nutritive fluid, contained in the innumerable vessels which penetrate nearly all of the tissues and organs of the body and are connected with the system of lymphatic and lacteal vessels. Second, the process by which the blood is circulated, sent by the heart to all parts in the capillary system, used by the tissues for their nutrition, then losing oxygen, gaining carbonic acid, and being returned by the veins. Third, respiration, the blood being freed from carbonic acid and getting a new supply of oxygen in the lungs, by which it is rendered capable of again circulating through the general system. Fourth, as the blood, in its passage through the capillary vessels, not only loses oxygen, but is more or less impoverished by the

assimilation of its nutritive constituents by the tissues, it is necessary to keep it up to the proper nutritive standard; and this is effected by alimentation, digestion, and absorption. Fifth, we have certain secretions, necessary to the above-mentioned processes; and the products of physiological waste or decay of the tissues are removed by excretion. Sixth, the processes of vegetative life involve the production of heat, and are regulated and coördinated by the nervous system.

The second class of functions relates to animal life, and these are called the functions of relation. In this class, are included movements, voice and speech, the functions of the cerebro-spinal nervous system, and the operation of the special senses.

In studying the processes of nutrition of the general system, we observe that certain constituents of the organism, which contain nitrogen and are exclusively of organic origin, have the property, in the living body, of self-regeneration; *i. e.*, when these parts are brought in contact with nutritive matter in proper form, as it exists in the blood, this matter is appropriated and transformed into the substance of each tissue and organ. It is in this way that, during adult life, the different parts of the organism are maintained in a tolerably uniform condition. In the absence of an exact knowledge of the cause and nature of these assimilative processes, we call them vital; which term is applied to a constant property of living, organized parts. Physiologists have ascertained that each tissue and organ of the body possesses one or more characteristic organic nitrogenized constituents which are possessed of this so-called vital property. But, at the same time, it is always observed that the organic nitrogenized constituents of the organism are combined most intimately with a tolerably-definite quantity of inorganic matter, which latter regulates, to a certain extent, the nutritive processes, and constitutes, also, an important component part of the tissues. It is observed, in addition, that, during early life, when the system is proceeding toward its perfect development by growth, the

proportion of inorganic matter is less than in the adult, and that the process of nutrition is then at its maximum of activity, the regeneration being superior to the waste. During the adult period, repair and physiological decay are nearly balanced; but, in the decline of life, there seems to be a gradual accumulation of inorganic matter, and this continues until the so-called vital properties of some important organ become so feeble that its functions cease, and we have physiological death. This regeneration of the tissues is a necessary consequence of the constant waste or decay of every part of the organism, resulting in a change of constituents into effete matters, which are discharged; there being, during life, a constant waste and repair. If no new matter be introduced as food, the system wastes to a point which is incompatible with life, and death results from inanition.

With some very insignificant exceptions, we cannot conceive that living tissues exist in an absolutely stationary condition. The organized parts of the body are undergoing constant molecular destruction and repair. Again, the so-called vital properties of the tissues, which involve self-regeneration, seem to have certain limits. We cannot introduce nutritive matter in sufficient quantity to produce growth beyond a certain point, though we may limit development and growth by deficient supply. When we ask why the organs develop with fixed regularity, why, when an occasional excess of nutritive matter is presented, this excess is not used, we must confess our ignorance, or say that the parts are endowed with vital properties. We also find, to come to the most important point of this discussion, that, however carefully we may supply nutritive matter to the system, we cannot arrest the gradual enfeeblement of the assimilative powers of the tissues, which occurs in old age. In short, as we cannot conceive of a living tissue without decay and regeneration of its substance, so it is impossible for the organism to last for an indefinite period. A necessary, invariable, and inevitable consequence of individual life is death. The constant molecular

death—if we can apply this term to the transformation of living into effete matter—of every tissue of the body is always, in the end, superior to the power of repair. There seems, indeed, to be an antagonism of processes during life; a view so fully adopted by Bichat, that it led to his celebrated definition of life; "the *ensemble* of functions which resist death."[1] Although death is thus inevitable, and, in the circulation of material in Nature, the organic parts of the body become changed in the arrangement of their ultimate elements and appropriated by the vegetable kingdom, during adult life, certain anatomical elements, male and female, are formed in the human subject, which, when they come together under proper conditions, develop into new beings, who pass through the same course of existence as the parents. By the concourse of two beings, new organisms come into life, which perpetuate existence and preserve species. The function by which this is accomplished is called generation, or reproduction.

In our study of generation, we shall confine ourselves as closely as possible to the process as it takes place in the human subject. There are many considerations of great interest connected with the generation of the lowest orders of animal organization, among the most prominent of which is the question of so-called spontaneous generation. While this may have a certain bearing upon the genesis of anatomical elements, it has little or nothing to do with the development of the fecundated human ovum, and will, therefore, receive little more than an incidental consideration. For similar reasons, we shall not engage in a discussion of the development-theory applied to the origin of species, which is exciting so much controversy at the present day, nor shall we treat of genera-

[1] BICHAT, *Recherches physiologiques sur la vie et la mort*, Paris, 1829, p. 2.

We do not quote Bichat's definition of life as one which we can unreservedly adopt. For more elaborate reflections on this point, the reader is referred to another volume, under the head of Nutrition. See vol. iii., Secretion, Nutrition, Movements, p. 369.

tion in the lower animals, except to illustrate the history of development in man.

The study of human generation will naturally assume the following course: First, the female organs of generation, and the formation of the female element, the ovum; second, the discharge of the ovum and the phenomena which attend this process; third, the male organs, and the development and discharge of the male elements, spermatozoids; fourth, the union of the two elements of generation, or fecundation; fifth, the development of the fecundated ovum into the fœtus at term; sixth, the development of the body after birth and at different ages, or stages of existence; finally, the natural cessation of the so-called vital functions, or physiological death.

Sexual Generation.

Before we describe the actual phenomena of sexual generation, as they are observed in man and the mammalia, it will be interesting to note some of the salient points in the history of our knowledge of this process in the inferior animals. This we can do, without exceeding the limits we have laid down in our general remarks.

In the history of sexual generation, there seems to have been a limiting line between the production of animals from preëxisting organisms and of those produced in some unknown manner, or, as it has been said, spontaneously. This line of distinction has always receded toward organisms lower and lower in the scale of being with our advance in positive knowledge. The ancients understood that the higher animals required for their production a concourse of the sexes; but they thought that many fishes, reptiles, insects, worms, etc., were produced spontaneously. Indeed, with the limited knowledge of natural history possessed by Aristotle and those who succeeded him for many hundred years, the classes of animals said to be produced spontaneously represented simply those, the generation of which was not understood. But, as the habits of many animals became better understood,

more and more of them were observed to lay eggs, which were found to undergo development.

Dating from Aristotle, who lived between three and four hundred years B. C., it was nearly two thousand years before any thing was known of the generation of insects; the difficulty here being that the young are first in a larval state and bear no resemblance to the parents. Anterior to the experiments of Redi, it was thought that certain organic matters in course of putrefaction developed living organisms, as maggots in meat and the larvæ in cheese.

We refer to the experiments of Redi, made about the year 1668, for the reason that these mark an era in our knowledge of the process of generation. This observer, noting that flies frequently lighted upon meat when it was exposed, simply protected it by gauze, and found that no maggots were developed, while other pieces of meat, placed under the same conditions, except that the flies had free access to them, developed maggots in great numbers.[1] By this simple experiment, Redi showed that the maggots in putrefying meat were produced by insects and not by the meat; but it remained for Swammerdam and Vallisneri[2] to study the metamorphoses of insects, and to show how the eggs were developed, first into sexless larvæ, and finally into perfect beings resembling the parents. It is curious to note the condition of science anterior to Redi and Vallisneri, and compare it with the ideas that are current at the present day. When maggots appeared in putrefying meat, they were thought to be produced by a spontaneous aggregation of organic particles, simply because observers knew of no other way in which these beings could come into existence. Now, the advocates of spontaneous generation have the same ideas as those advanced anterior to 1668; but, in the place of meat, they have organic infusions, and for maggots, they substitute infusorial animalcules. It is possible that the discus-

[1] REDI, *Experimenta circa Generationem Insectorum*, Amstelædami, 1686, p. 40.

[2] VALLISNERI, *Istoria della Generazione*, Venezia, 1721, p. 19.

sion of the question was as energetic as it is now; but the positive advances in a knowledge of the generation of insects has swept away the memory of such discussions, if they existed, as future advances may possibly cause many of the controversial writings of the present day to pass into oblivion.

For a time after the researches to which we have just alluded had taken their place in the history of science, there was little written about spontaneous generation. Redi had satifactorily described the mode of generation of many of the entozoa, the origin of which had been obscure; Harvey had enunciated, in substance, his famous axiom "*omne animal ex ovo;*"[1] Regnerus de Graaf had described, in the ovaries, the vesicles which have since borne his name;[2] and the knowledge of ovulation and development began to make definite progress, the important fact having been ascertained, that viviparous, as well as oviparous animals, are produced from ova.

With the discovery, by Leeuwenhoek,[3] of living beings in water, called by him animalcules, but since known as infusoria, a new problem was presented to students of natural history. Here were animal organisms, so small as to be invisible to the naked eye, existing in great variety and in infinite numbers, the mode of generation of which was not un-

[1] HARVEY, *Exercitationes de Generatione Animalium*, Londini, 1651. On page 2, is the following: "omnia omnino animalia, etiam vivipara, atque hominem adeò ipsum ex ovo progigni." This quotation is from the original edition of Harvey's work. In the life of Harvey, by Robert Willis, published in the Sydenham edition of the works, London, 1847, p. lxix., is the following: "He announced the general truth: Omne animal ex ovo." It is probable that this is the passage from which the familiar quotation is made.

[2] DE GRAAF, *De Mulierum Organis Generationi inservientibus Tractatus Novus*, Lugd. Batav., 1672, p. 177. On p. 181, is the following: "Ova in omni animalium genere reperiri confidentur asserimus; quandoquidem ea non tantùm in avibus, piscibus tam oviparis quàm viviparis; sed etiam in quadrupedibus, ac homine ipso evidentissimè conspiciantur."

[3] LEEUWENHOEK, *Concerning little Animals by him observed in Rain- Well- Sea- and Snow-water; as also in water wherein Pepper had lain infused.—Philosophical Transactions*, London, 1677, No. 133, p. 821, *et seq.* The observations referred to were made in 1675.

derstood. As these organisms were studied more closely, their multiplication by segmentation and by budding became known, and these have since been described as processes of generation peculiar to some of the lower orders of beings; but, at the same time, some writers revived the theory of spontaneous generation, to account for the original appearance of animalcules in water, and this idea has its advocates at the present day. If, however, we follow out the history of the spontaneous-generation theory, we find that the different epochs have repeated themselves; that the theory took its origin from an ignorance of the mode of generation of organisms quite high in the scale of being; that the progress of exact knowledge gradually restricted the theory to lower and lower organisms, until, by this rigid process, it became extinct, simply from want of material; that its application to entozoa was eliminated in the same way; that it was revived by the discovery of infusoria; and that now its limits have been restricted by positive advances in knowledge, it being demonstrated, by Balbiani and others, that many varieties of infusoria present the phenomena of sexual generation.[1]

Of the advocates of spontaneous generation within a comparatively recent period, perhaps the most prominent has been Pouchet;[2] but modern researches have shown pretty clearly that the infusoria produced in organic infusions are due, in all probability, to the introduction of ova, or spores floating in the air, which are developed when they meet with proper conditions of heat and moisture. In numerous experiments by different observers, which it is not necessary to cite in detail, it appeared that, when organic infusions had been exposed to a degree of heat sufficient to destroy germs, and the introduction of new germs from the air was pre-

[1] BALBIANI, *Recherches sur les phénomènes sexuels des infusores.—Journal de la physiologie*, Paris, 1861, tome iv., pp. 102, 194, 431, 465.

[2] POUCHET, *Théorie positive de l'ovulation spontanée*, etc., Paris, 1847. This was followed by numerous other publications by Pouchet, and the views advanced excited a most animated discussion in France and elsewhere, which continued for several years.

vented, no infusoria were developed; and this was the case when air was admitted to the infusions, care being taken to pass the air through heated tubes or sulphuric acid, so as to destroy all organic matter. The present aspect of the question of spontaneous generation is the following:

First, it is reduced to the very lowest orders of infusoria, such as vibriones and bacteria, which simply present movement, have no distinguishable internal structure, and are exceedingly minute.

Second, the question is discussed as to what degree of temperature and length of exposure to heat are necessary in order to destroy preëxisting germs in organic infusions; for the idea that living organisms ever result from an aggregation of inorganic particles has been generally abandoned, and the so-called spontaneous production of animals has been reduced to a coming together of organic molecules.

It is at once apparent to the rigidly scientific mind that the second division of the question presents great difficulties in the way of its positive solution. It is granted, for example, that vibriones and bacteria are living, animal organisms. It is proposed by the advocates of the theory of spontaneous generation, that these beings arise without preëxisting germs, by an aggregation of organic particles. The opponents of this view assert that, when the air admitted to organic infusions is freed from germs or organic particles, and when the organic infusions are subjected to a high temperature for a time sufficient to destroy all possible preëxisting germs, no generation of infusoria can take place. Now, what degree of temperature is required, what is the duration of exposure to heat necessary to destroy germs, and how are the limits of these conditions to be ascertained?[1] The only

[1] Upon this point, we may refer to the admirable and entirely conclusive experiments of Wyman. His conclusions, as far as they bear upon the question under consideration, are the following:

"1st. In thermal waters plants belonging to the lower kinds of Algæ live in water the temperature of which in some instances rises as high as 208° Fahr.

"2d. Solutions of organic matter boiled for twenty-five minutes, and exposed

answer to this question lies in the experimental test. When infusoria make their appearance in solutions that have been exposed to heat and protected from the entrance of germs, it is said that the heat has not been sufficiently high or the exposure has been of too short duration. When infusoria do not appear, the conditions are assumed to have been fulfilled. This mode of reasoning assumes the fact, from the beginning, that there is no such thing as spontaneous generation. Suppose, now, we start with the contrary assumption, that there may be spontaneous generation in an organic infusion. We admit to such an infusion, air, carefully purified from germs, which is logically an essential experimental condition; we have previously exposed the infusion to a high temperature for a certain period. Under these conditions, no infusoria appear. It may then be assumed that the heat has destroyed the properties of the organic molecules, so that they cannot come together and generate new beings.

Under these circumstances, all that we can do is to argue logically from such facts as have been positively established, and to take the most reasonable view of other points, that are not as yet capable of satisfactory and definite explanation.

We shall assume that it has been demonstrated, beyond a reasonable doubt, that, in organic infusions, subjected to a temperature somewhat above that of boiling water, and supplied with air that has been effectually deprived of organic

only to air which had passed through iron tubes heated to redness, became the seat of infusorial life. Exps. i.–v.

"3d. Similar solutions contained in flasks hermetically sealed, and then immersed in boiling water for periods varying from a few minutes to four hours, also became the seat of infusorial life. The infusoria were chiefly Vibrios, Bacteriums, and Monads. Exps. vi.–xv.

"4th. No ciliated infusoria, unless Monads are such, appeared in the experiments referred to in the above conclusions.

"5th. No infusoria of any kind appeared if the boiling was prolonged beyond a period of five hours."

(JEFFRIES WYMAN, *Observations and Experiments on Living Organisms in Heated Water*, New Haven, 1867, p. 20. From the *American Journal of Science and Arts*, vol. xliv., September, 1867.)

matter, ova, spores, or whatever it may be, no living organisms make their appearance so long as these experimental conditions are maintained. We also assume that simple boiling, at 212° Fahr., does not necessarily destroy all germs, which excludes experiments made in this way. This reduces the question to a single, simple point: In infusions in which the organic matter has not been destroyed by heat, do the living organisms come from a spontaneous aggregation of organic molecules, or are they the result of the development of ova?

In the case of the very lowest organisms making their appearance under these conditions, they are themselves so small, that it would be reasonable to suppose that we might be unable to see the ova, assuming that they exist. The organic particles that are supposed to come together spontaneously are also invisible, even under the highest magnifying powers at our command. If we come to an exact definition of the term spontaneous, we may say that it means an action "arising or existing from natural inclination, disposition, or tendency, or without external cause" (Worcester). With this definition, the statement that a living organism is generated spontaneously can only mean that there is no cause that can be assigned for its production. In point of fact, we simply acknowledge that the mode and cause of generation of certain infusoria are unknown, and the history of our knowledge of generation shows that the term spontaneous generation has always been applied to the production of beings in a manner that is incapable of satisfactory explanation. What we actually know of the mode of generation of animal organisms teaches us that all beings are produced and multiplied by ova, or by processes of segmentation or budding of preëxisting organisms; and our knowledge of these processes now extends to all except the most minute infusoria, which have no apparent structure. We know, also, that such organisms may develop in pure water from particles floating in the atmosphere; and that particles in the air, singly invisible, may be developed

into infusoria that are quite highly organized. If we reason that the products of so-called spontaneous generation are formed by the fortuitous aggregation of organic molecules, we assume a fact of which we have no other example in Nature; and we assume, also, that such an aggregation of particles produces beings of a definite and uniform character. For such a supposition, we have no basis in analogy. If, on the other hand, we regard these low orders of beings as produced by the development of invisible germs, which have found favorable conditions of heat and moisture, we rest upon a basis of reasonable analogy, and merely confess that this is a form of generation, the processes of which are not as yet capable of demonstration.

As the only true philosophic view to take of the question, we shall assume, in common with nearly all modern writers on physiology, that there is no such thing in Nature as spontaneous generation; admitting that the exact mode of production of some of the infusoria, lowest in the scale of being, is not understood.

Female Organs of Generation.

An accurate knowledge of certain points in the anatomy of the female organs of generation is essential to the comprehension of the most important of the processes of reproduction. Following a fruitful intercourse of the sexes, the function, as regards the male, ceases with the comparatively simple process of penetration of the male element through the protective covering of the ovum, and its fusion with the female element. The fecundated ovum then passes through certain changes, which are the first processes of its development, forms its attachments to the body of the mother, continues its development, materials being derived from the mother, is nourished and grows, until the fœtus at term is brought into the world. An exact knowledge of the mechanism of these complicated processes can only be obtained after a careful study of the anatomy of the female organs

We must know precisely how the ovum is developed in the ovary and how it is discharged; how, after its discharge, it is received by the oviduct and carried to the uterus; if fecundation do not take place, there is nothing more to study, as the ovum is lost; but, as the fecundated ovum must form certain attachments within the uterus, we must be acquainted with the anatomy of this organ, before we can comprehend its development. Again, we have to study the phenomena which attend the discharge of ova, and the changes which take place in the ovaries, anterior to, during, and subsequent to ovulation. It will not be essential for us to study very closely the anatomy of the external parts, as these are only concerned in sexual intercourse and in parturition; which latter, though a purely physiological process, forms the greatest part of the science of obstetrics, is considered elaborately in treatises on this subject, and is not usually treated of, to any great extent, in physiological works.

The female organs of generation are divided anatomically into internal and external. The external organs are the vulva, and adjacent parts, and the vagina; the internal organs are the uterus, Fallopian tubes, and ovaries. When we come to study the functions of the internal parts, we shall see that the ovaries are the true female organs, in which, and in which alone, the female element can be produced. The Fallopian tubes and the uterus are accessory in their functions, the female element, the ovum, passing through the Fallopian tubes to the uterus, where it forms the attachments to the body of the mother which are essential to its nourishment and full development after fecundation.

Before we proceed to study the structure of any of the female organs, it is important to have a clear idea of the general arrangement and the relations of these parts; for, without this, we shall be constantly in the dark as to the bearing of certain important anatomical points that have been brought forward within the last few years.

The vagina has a direction, slightly curved anteriorly,

which is nearly coincident with the axis of the outlet, or the inferior strait of the pelvis. Projecting into the vagina, at its upper extremity, is the lower part of the neck of the uterus. The uterus extends from the vagina nearly to the brim of the pelvis. It is situated between the bladder and the rectum, and has an antero-posterior inclination, when the bladder is moderately distended, which brings its axis nearly coincident with that of the superior strait of the pelvis.[1] Supposing the body to be erect, the angle of the uterus with the perpendicular would be about forty-five degrees. These details with regard to the position of the uterus are essential to a comprehension of the situation and relations of the ovaries and Fallopian tubes.

The uterus is held in place by ligaments, certain of which are formed of folds of the peritoneum. The anterior ligament is reflected from the anterior surface to the bladder; the posterior ligament extends from the posterior surface to the rectum; the round ligaments extend from the upper angle of the uterus, on either side, between the folds of the broad ligament and through the inguinal canal, to the symphysis pubis; the broad ligaments, which extend from the sides of the uterus to the walls of the pelvis, are the most interesting of all, as they lodge the ovaries and the Fallopian tubes.

If we imagine the uterus, occupying, as it does, the upper part of the pelvis, and remember its angle of inclination, it is evident that it, with the broad ligaments, must partially divide the pelvis into two portions; and these ligaments, which are formed of a double fold of peritoneum, present a superior, or posterior surface, and an inferior, or anterior surface. The superior, or anterior border of this fold is

[1] The statements given above, with regard to the position of the uterus, are very general. The uterus is exceedingly movable antero-posteriorly, and the direction of its axis is largely dependent upon the condition of the other pelvic organs. When the bladder is distended, the fundus is moved upward; and, when the bladder is empty, the axis of the uterus may be inclined forward so as to become nearly horizontal.

occupied by the Fallopian tubes, the peritoneum constituting their outer coat; laterally, at the free extremities of the tubes, the peritoneum ceases, and there is an actual opening of each tube into the peritoneal cavity. Attached to the broad ligament, and projecting upon its posterior surface, is the ovary. This little, almond-shaped body is connected with the fibrous tissue between the two layers of the ligament, and has no proper peritoneal investment; so that it is actually within the peritoneal cavity. If we look at the ovary from the front, we simply see the rounded prominence which marks the point of attachment to the broad ligament; but, if we look from behind, the projecting surface is seen, and we have a distinct ring of demarcation at the base, which indicates where the tessellated, serous epithelium ceases, and where the proper columnar epithelium of the ovary begins. If a vesicle should rupture upon the surface of the ovary, its contents might thus be taken up by the Fallopian tube and be carried to the uterus. Each ovary is attached to the uterus by a ligament, lying just beneath the peritoneum, called the ligament of the ovary. This ligament is composed of non-striated muscular fibres. Between the folds of the broad ligament, are, the round ligament of the uterus, vessels, nerves, and a thin layer of non-striated muscular fibres continuous with the superficial muscular fibres of the uterus.

We are now prepared to study Fig. 24, which shows the general arrangement of these parts, viewed from behind. A portion of the figure which, in the original, shows the external parts, is cut off, to avoid complicating our description. The left half is represented as covered with peritoneum, and the free, fimbriated extremity of the Fallopian tube on this side is drawn away from the ovary, leaving only a single prolongation, which is attached. This shows that the Fallopian tube opens directly into the peritoneum, and that the ovary is also actually in this cavity, and has no true peritoneal covering. On the right side, the posterior layer of the

broad ligament and the posterior peritoneal covering of the uterus have been removed. On this side, the extremity of the Fallopian tube is applied to the ovary. The exact relations between the ovaries and the Fallopian tubes will be discussed hereafter, but Fig. 24 shows how the extremity

FIG. 24.

1, the uterus, on the left, with the peritoneal covering, and, on the right, this covering removed; 2, vaginal portion of the uterus; 6, left Fallopian tube, with its abdominal opening free, and with one fimbria attached to the ovary; 7, right Fallopian tube, with its fimbriæ grasping the ovary; 8, parovarium; 9, ovary; 10, ligament of the ovary; 11, ala vespertilionis (portion of the broad ligament between the ovary and the Fallopian tube); 12, broad ligament of the uterus; 13, the so-called internal spermatic artery, or ovarian artery; 14, the uterine artery; 15, round ligament of the uterus. (LUSCHKA, *Anatomie des Menschen*, Tübingen, 1864, Bd. ii, S. 328.)

may be applied to the ovary. On the left side, are seen the two layers of the broad ligament. A careful examination of this figure will give a general idea of the relations of the different parts and enable us to study intelligently their minute anatomy.

The Ovaries.—The situation of these bodies has already been indicated. Attached, as they are, to the broad ligament, and projecting from its posterior surface, they lie nearly horizontally in the pelvic cavity, on either side of the uterus. They are of a whitish color, and their form is ovoid and flattened, with the anterior border, sometimes called the base, attached to the broad ligament. If we closely examine their mode of connection with the broad ligament, it is seen

that, at the margin of the attached surface of the ovary, the posterior layer of the ligament ceases, and that the fibrous stroma of the medullary portion of the ovary is continuous with the fibrous tissue lying between the two layers. It is at this portion of the ovary, called the hilum, that the vessels penetrate, to be distributed in its substance.

Each ovary is about an inch and a half in length, half an inch in thickness, and three-quarters of an inch in width at its broadest portion. The outer extremity is somewhat rounded, and is attached to one of the fimbriæ of the Fallopian tube. The inner extremity is more pointed, and is attached to the side of the uterus by means of the ligament of the ovary. This ligament is shown in Fig. 24 (10). It is a rounded cord, composed of non-striated muscular fibres spread out upon the attached extremity of the ovary and the posterior surface of the uterus, and is covered by peritoneum. The weight of each ovary is from sixty to one hundred grains, and these organs are largest in the adult virgin. Its attached border is called the hilum; and, at this portion, the vessels and nerves penetrate. The surface is marked by rounded, translucent elevations, produced by distended Graafian follicles; and we frequently see here little cicatrices, indicating the situation of ruptured follicles. We may also see, between the distended follicles, corpora lutea in various stages of atrophy.

Within the last few years, anatomical researches have shown that the surface of the ovaries does not present the appearance of a continuation of the peritoneum. At the base, is a distinct line, surrounding the hilum, which indicates where the peritoneum ceases and where the proper epithelial covering of the ovary begins; and there is a well-marked and abrupt distinction between the tessellated epithelium of the serous surface and the layer of cylindrical cells covering the ovary itself. This peculiarity has given rise to the idea that the ovary is really covered by a mucous membrane. Indeed, there seems to be little difference between the cells covering

the ovaries and those lining the Fallopian tubes, except that the latter are provided with cilia.[1]

Most anatomists describe a proper fibrous membrane investing the ovaries, which they call the tunica albuginea, and which is compared to the fibrous covering of the testes. This, however, is not a proper term. Sappey denies the existence of a tunica albuginea;[2] and, indeed, in the sense in which it was formerly described, such a membrane cannot be demonstrated. On making a section of the ovary, it is readily seen by the naked eye that the organ is composed of two distinct structures; a cortical substance, formerly called the tunica albuginea, which is about $\frac{1}{25}$ of an inch in thickness, and a medullary substance, containing a large number of blood-vessels. The cortical substance alone contains the Graafian follicles. The external layer of this may be a little denser than the deeper portion, but there is no distinct fibrous membrane.

The structure of the cortical substance of the ovary is very simple. It consists of connective tissue in several layers, the fibres of which are continuous with the looser fibres of the medullary portion. In the substance of this layer, are embedded the ova, enclosed in the sacs, called Graafian follicles. This layer contains a few blood-vessels, coming from the medullary portion, which surround the follicles.

The medullary portion is exceedingly vascular, and is composed of numerous small bands, or trabeculæ of connec-

[1] It appears that Koster was the first to give an account, in 1868, of the true structure of the epithelium on the surface of the ovaries. Waldeyer, according to a late review of recent works on the ovary and ovum, is said to have made this discovery simultaneously with Koster. (CLAPARÈDE, *L'ovaire et l'œuf.—Revue des cours scientifiques*, Paris, 1870, tome vii., p. 662.) In the list of works given in this review by Claparède, the date of Koster's article is 1868; and Waldeyer's researches were published in 1870. We have not been able to consult the original paper by Koster, published in Dutch. Waldeyer gives a very clear description of the epithelium, in his article contributed to Stricker's "Histology." (WALDEYER, in STRICKER, *Manual of Human and Comparative Histology*, The New Sydenham Society, London, 1872, vol. ii., p. 166.)

[2] SAPPEY, *Traité d'anatomie*, Paris, 1874, tome iv., p. 688.

tive tissue, with smooth muscular fibres. The blood-vessels, which penetrate at the hilum, are large and convoluted, especially at the hilum itself, where there is a mass of convoluted veins, forming a sort of vascular bulb, which has been described particularly by Rouget. In the medullary portion of the ovary, which is sometimes called the vascular zone, the muscular fibres follow the vessels, in the form of muscular sheaths. According to Rouget, the mass of vessels at the hilum constitutes a true erectile organ.[1]

In addition to the blood-vessels, the ovary receives nerves from the spermatic plexus of the sympathetic, the exact mode of termination of which has not been ascertained. Lymphatics have also been demonstrated at the hilum.

Graafian Follicles.—These vesicles, or follicles, were described and figured by De Graaf, and are known by his name.[2] They contain the ova, undergo a series of interesting changes, enlarge, approach the surface of the ovary, and finally are ruptured, discharging their contents into the fimbriated extremity of the Fallopian tube.

It was formerly supposed that the smallest Graafian follicles were situated deeply in the medullary portion of the ovaries, approaching the surface gradually, as they became larger; but it is now known that they are developed exclusively in the cortical substance. If, indeed, we examine the ovary at any period of life, we find no follicles properly in the medullary substance; but a few of the larger may project downward, so as to encroach somewhat upon it, being actually of a diameter greater than the thickness of the cortex.

The earlier anatomists supposed that the Graafian follicles were few in number, fifteen or twenty, but they counted those only that were readily seen with the naked eye. When, however, it was calculated that ova might be discharged

[1] Rouget, *Recherches sur les organes érectiles de la femme.—Journal de la physiologie*, Paris, 1858, tome i., p. 320, *et seq.*

[2] Regnerus de Graaf, *De Mulierum Organis Generationi inservientibus Tractatus Novus*, Lugd. Batav., 1672, p. 190.

every month during a period of about forty years, it became evident that the follicles must either be quite numerous, or become successively and constantly developed. This led some anatomists, who believed that, at the age of puberty, the ovaries contained, either partially or fully developed, all the follicles that ever existed in these organs, to increase their estimates of the number of follicles. Sappey, from a series of careful observations on this point, puts the number of follicles at from 600,000 to 700,000.[1] We cannot but regard this estimate as very much exaggerated. According to the table of measurements given by Waldeyer, the primordial follicles in the human embryo, at the seventh month, measure from $\frac{1}{800}$ to $\frac{1}{250}$ of an inch, and the primordial ova, from $\frac{1}{1650}$ to $\frac{1}{1000}$ of an inch.[2] From what has been written on this point, it seems difficult, if not impossible, to give an approximation, even, of the number of follicles in the ovaries, but there certainly must be several thousands, many of which may never become fully developed.

Within the last few years, very important advances have been made in our knowledge of the mode of development of the ova and ovaries, which will be more fully considered hereafter; but we must here refer to these points briefly, in order to give a clear idea of the relations of the Graafian follicles, in the different forms which they present under varied conditions of development.

The ovary appears, particularly from observations on the development of the chick, very early in embryonic life, in the form of a cellular outgrowth from the Wolffian body. Most of its cells are small, but, as early as the fourth or fifth day, some of them are to be distinguished by their large size, their rounded form, and the presence of a large nucleus. These cells are supposed to be primordial ova. In the process of development of the ovary, some of the peripheral cells pene-

[1] SAPPEY, *Traité d'anatomie*, Paris, 1874, tome iv., p. 694.

[2] WALDEYER, in STRICKER, *Manual of Human and Comparative Histology*, The New Sydenham Society, London, 1872, vol. ii., p. 207.

trate in the form of tubes, the so-called ovarian tubes, and, at the same time, delicate processes, formed of connective tissue and blood-vessels, extend from the fibrous stroma underlying the epithelium and enclose collections of cells. It is probable that we have these two modes of formation of follicles; one, by the penetration of epithelial tubes from the surface, which become constricted and divided off into closed cavities, and the other, by the extension of fibrous processes from below, which enclose little collections of cells. By both of these processes, little cavities are formed, which contain a number of cells. In each of these cavities, we observe a single, large, rounded cell, with a large nucleus, this cell being a primordial ovum; and, in addition, we have, in the same cavity, other cells, which are the cells of the Graafian follicle. The exact nature of the processes we have just described has been studied in the fowl, but it is probable that the same kind of development occurs in mammalia and in the human female.

From birth until just before the age of puberty, the cortical substance of the ovary contains thousands of what are termed primordial follicles enclosing the primordial ova; and it is probable that, after the ovaries are fully developed at birth, no additional ova or Graafian follicles make their appearance. The prevailing idea is, indeed, that the great majority of these never arrive at maturity, and that they undergo atrophy at various stages of their development. According to the table of measurements given by Waldeyer, from whose article most of the facts we have stated have been taken, the primordial follicles of the human embryo, at the seventh month, are from about $\frac{1}{300}$ to $\frac{1}{250}$ of an inch in diameter, and the primordial ova, from $\frac{1}{1650}$ to $\frac{1}{1000}$ of an inch. In the adult, the smallest follicles measure from about $\frac{1}{300}$ to $\frac{1}{600}$ of an inch, and the smallest ova, a little more than $\frac{1}{1000}$ of an inch.[1] The primordial ova have the form of rounded cells, each with a large, clear nucleus, and a nucleolus. Other

[1] WALDEYER, in STRICKER, *Manual of Human and Comparative Histology*, The New Sydenham Society, London, 1872, vol. ii., p. 207.

structures are developed in and surrounding these cells, as they arrive at their full development.

The most interesting stage in the development of the ova and Graafian follicles is observed at about the period of puberty. At this time, a number of follicles, twelve, twenty, thirty, or even more, enlarge, so that we have all sizes, between the smallest primordial follicles, $\frac{1}{800}$ of an inch, and the largest, nearly $\frac{1}{2}$ an inch in diameter. In follicles that have attained any considerable size, we have the fully-developed ova, one in each follicle, except in very rare instances, when there are two,[1] and these ova have a pretty uniform diameter of about $\frac{1}{125}$ of an inch. In the process which culminates in the discharge of the ovum into the fimbriated extremity of the Fallopian tube, the Graafian follicle gradually enlarges, becomes distended with liquid, and finally breaks through and ruptures upon the surface of the ovary. It becomes necessary, then, to study the structure of these large follicles and their relations to the ova; but, before we do this, we can review, with advantage, the relations of the different portions of the ovary and the follicles and ova of various sizes, by an examination of Fig. 25.

Fig. 25 shows the follicles and ova of various sizes. It is observed that the larger follicles contain fully-formed ova, and have a proper fibrous coat. The ova here present an epithelial covering, and are embedded in a mass of the epithelial lining of the follicle (membrana granulosa), this mass being called the discus or cumulus proligerus.

According to the measurements given by Waldeyer,[2] the

[1] Schrön has observed two and even three ova in a single follicle, in some of the lower animals. In four hundred examinations of ovaries of the cat, he found one follicle with two, and one follicle with three ova. In eighty examinations in the bitch, he found a single follicle with two ova; but he found no other examples of this. (SCHRÖN, *Beitrag zur Kentniss der Anatomie und Physiologie des Eierstocks der Säugethiere.—Zeitschrift für wissenschaftliche Zoologie*, Leipzig, 1863, Bd. xii., S. 409, *et seq.*) Kölliker noted two ova in a single follicle, in the human subject. (*Éléments d'histologie humaine*, Paris, 1868, p. 705.)

[2] WALDEYER, in STRICKER, *Manual of Human and Comparative Histology*, The New Sydenham Society, London, 1872, vol. ii., p. 207.

smallest Graafian follicles are from $\frac{1}{300}$ to $\frac{1}{200}$ of an inch in diameter, while the largest measure from $\frac{3}{8}$ to $\frac{1}{2}$ an inch. At or near the period of their maturity, the follicles present several coats and are filled with an albuminous liquid. The ma-

Fig. 23.

Portion of a sagittal section of the ovary of an old bitch.—*a*, ovarian epithelium; *b*, *b*, ovarian tubes; *c*, *c*, younger follicles; *d*, older follicle; *e*, discus proligerus, with the ovum; *f*, epithelium of a second ovum in the same follicle; *g*, fibrous coat of the follicle; *h*, proper coat of the follicle; *i*, epithelium of the follicle (membrana granulosa), follicle collapsed and degenerated; *l*, vessels; *m*, *m*, cell-tubes of the parovarium, divided longitudinally and transversely; *y*, tubular depression of the ovarian epithelium in the tissue of the ovary; *z*, beginning of the ovarian epithelium close to the lower border of the ovary. (WALDEYER, in STRICKER, *Handbuch der Lehre von den Geweben*, Leipzig, 1871, S. 545.)

ture follicles project just beneath the surface and form little rounded, translucent elevations; the smallest follicles are near the surface, and, as they enlarge, at first become deeper, as is seen in Fig. 25, becoming superficial only as they approach the period of fullest distention.

Taking one of the largest follicles as an example, two fibrous layers can be distinguished; an outer layer, of ordinary connective tissue, and an inner layer, the tunica propria, formed of the same kind of tissue, with the difference that, as the follicle enlarges, the inner layer becomes vascular.[1] The vascular tunica propria is lined by cells of epithelium, forming the so-called membrana granulosa. At a certain point in this membrane, is a mass of cells, called the discus or cumulus proligerus, in which the ovum is embedded. The situation of the discus proligerus and the ovum has been a subject of discussion; some describe it in the most superficial portion, and others, in the deepest part of the follicle. Waldeyer states that he has observed it in both situations;[2] and it is probable that its position is not invariable.

The liquid of the Graafian follicle is alkaline, slightly yellowish, not viscid, and contains a small quantity of albuminoid matter coagulable by heat, alcohol, and acids.[3] This liquid is supposed to be secreted by the cells lining the inner membrane of the follicle.

[1] Some anatomists describe the two fibrous layers of the Graafian follicle as a single membrane; and some, who recognize the two layers, state that the outer layer alone is vascular. We have adopted the description of Waldeyer, as given above.

[2] WALDEYER, in STRICKER, *Manual of Human and Comparative Histology*, The New Sydenham Society, London, 1872, vol. ii., p. 174.

As early as 1847, Pouchet stated that, in numerous observations on the sow, the ovum was ordinarily found near the deepest portion of the Graafian follicle. (POUCHET, *Théorie positive de l'ovulation spontanée*, Paris, 1847, p. 48.) Among the more recent writers, we find that Schrön states that the ovum is almost always found at the deepest portion of the follicle. (*Beitrag zur Kentniss der Anatomie und Physiologie des Eierstocks der Säugethiere.—Zeitschrift für wissenschaftliche Zoologie*, Leipzig, 1863, Bd. xii., S. 419.)

[3] ROBIN, *Leçons sur les humeurs*, Paris, 1867, p. 385.

It is important to remember that the ovum is not a product of secretion, nor can the ovary be properly considered as a glandular organ. The ovum is an anatomical element; and the ovary is the only organ in which this anatomical element can

FIG. 26.

Graafian follicle. Magnified 30 diameters.—1, 1, stroma of the ovary; 2, 2, convoluted, cork-screw blood-vessels; 3, fibrous wall of the follicle; 4, membrana granulosa; 5, cumulus proligerus; 6, zona pellucida of the ovum; 7, vitellus of the ovum; 8, germinal vesicle with the germinal spot. (LUSCHKA, *Anatomie des Menschen*, Tübingen, 1864, Bd. ii., S. 326.)

be developed. The only process of secretion which takes place in the ovary is the production, probably by the cells of the membrana granulosa, of the liquid of the Graafian follicles.

The Parovarium.—The parovarium, or organ of Rosenmüller, which is shown in Fig. 24 (8), is simply the remains of the Wolffian body, lying in the folds of the broad ligament, between the ovary and the Fallopian tube. It consists of from twelve to fifteen tubes of fibrous tissue, lined by ciliated epithelium, and has no physiological importance. The Wolffian bodies will be fully described in connection with the development of the genito-urinary system.

The Uterus.—The form, situation, and relations of the uterus and Fallopian tubes have already been indicated,[1] and are shown in Fig. 24.

The uterus is a pear-shaped body, somewhat flattened antero-posteriorly, presenting a fundus, a body, and a neck. At its lower extremity, is an opening into the vagina, called the os externum. At the upper portion of the neck, is a constriction, which indicates the situation of the os internum.

Fig. 27.

Virgin uterus, completely isolated. (Seen from behind, two-thirds of the natural size.)—1, body; 2, neck; 3, 3, extremities of the Fallopian tubes; 4, os externum; 5, posterior, 6, anterior, lip of the vaginal portion. (Luschka, *Anatomie des Menschen*, Tübingen, 1864, Bd. ii., S. 347.)

Its form is shown in Fig. 27. It is usually about three inches in length, two in breadth, at its widest portion, and one inch in thickness. Its weight is from one and a half to two and a half ounces. It is somewhat loosely held in place by the broad and round ligaments and by the folds of the peritoneum in front and behind. The delicate layer of peritoneum which forms its external covering extends behind as far down as the vagina, where it is reflected back upon the rectum, and anteriorly, a little below the upper extremity of the neck (os internum), where it is reflected upon the urinary bladder. At

[1] See page 267.

the sides of the uterus, the peritoneal covering, a little below the entrance of the Fallopian tubes, becomes loosely attached, and leaves a line for the penetration of the vessels and nerves. Fig. 28, giving a view of the interior of the uterus, shows a triangular cavity, with two cornua, corresponding to the

FIG. 28.

Interior of the virgin uterus (two-thirds of the natural size).—1, cavity of the body of the uterus; 2, canal of the cervix uteri, with the arbor vitæ and ovules of Naboth; 3, os internum; 4, os externum; 5, 5, openings of the Fallopian tubes. (LUSCHKA, *Anatomie des Menschen*, Tübingen, 1864, Bd. ii., S. 349.)

openings of the Fallopian tubes, and exceedingly thick walls, the greatest part of which is composed of layers and bands of non-striated muscular fibres.

The muscular walls of the uterus are composed of fibres of the involuntary variety, arranged in several layers. These fibres are spindle-shaped, always nucleated, the nucleus presenting one or two large granules, which have been taken for nucleoli. They are closely bound together, so that they are isolated with great difficulty. In addition to an amorphous adhesive substance between the muscular fibres, we find numerous rounded and spindle-shaped cells of connective tissue of the variety called embryonic, and a few elastic fibres. The muscular tissue of the uterus is remarkable from the fact that the fibres enlarge immensely during gestation, becoming, at

that time, ten or fifteen times as long and five or six times as broad as they are in the unimpregnated state. They are united into bundles, or fasciculi, which, in certain of the layers, interlace with each other in every direction.

It is quite difficult to follow out the course of the fasciculi of the uterus, and the layers are described somewhat differently by different writers. All agree, however, that there is a superficial layer, tolerably distinct, very thin, resembling the platysma myoides, which is sometimes called the platysma of the uterus. In addition to this layer, we shall describe two; making, in all, three layers, an external, middle, and internal, though this division is somewhat arbitrary.

The external layer, very thin but distinct, is closely attached to the peritoneum. When the uterus is somewhat enlarged after impregnation, we observe oblique and transverse superficial fibres passing over the fundus and the anterior and posterior surfaces to the sides. Here they are prolonged into the Fallopian tubes, the round ligament, and the ligament of the ovary, and also extend between the layers of the broad ligament. This external layer is so thin that it cannot be very efficient in the expulsive contractions of the uterus; but, from its connections with the Fallopian tubes and the ligaments, it is useful in holding the uterus in place. It does not extend entirely over the sides of the uterus. Rouget, who has given a very elaborate description of the external layer in the human subject and in various classes of animals, has found it prolonged into the ligaments and extending to the ovaries and Fallopian tubes. He regards the uterus and its so-called appendages as lying between two thin, muscular sheets, and considers the action of the muscular fibres as very efficient in producing an engorgement of the erectile tissue of the internal organs, by constriction of the veins. Erection, according to this observer, occurs at the period of menstruation, determines the application of the fimbriated extremity of the Fallopian tubes to the surface of the ovary, and assists in the

expulsion of the ovum.[1] These points will be more fully considered under the head of ovulation.

The middle layer is the one most efficient in the parturient contractions of the uterus. It is composed of a thick and complicated net-work of fasciculi interlacing with each other in every direction.

The inner layer is arranged in the form of broad rings, which surround the Fallopian tubes, become larger as they extend over the body of the uterus, and meet at the centre of the organ near the neck.

The mucous membrane of the uterus is of a pale, reddish color; and that portion lining the body is smooth, and so closely attached to the subjacent structures, that it cannot be separated to any great extent by dissection. There is, however, no proper submucous areolar tissue, the membrane being applied directly to the uterine walls. It is covered by a single layer of cylindrical epithelial cells with delicate cilia, the movements of which are from without inward, toward the openings of the Fallopian tubes.[2] Examination of the surface of the membrane with a low magnifying power shows the openings of numerous tubular glands. These glands are usually simple, sometimes branched, dividing, about midway between the opening and the lower extremity, into two and, very rarely, into three secondary tubules. Their course is generally tortuous, so that their length frequently exceeds the thickness of the mucous membrane. The openings of these tubes are about $\frac{1}{350}$ of an inch in diameter.

The uterine tubes are of considerable physiological interest, and have been the subject of much discussion. Their secretion, which forms a thin layer of mucus on the surface

[1] ROUGET, *Recherches sur les organes érectiles de la femme.—Journal de la physiologie*, Paris, 1858, tome i., pp. 320, 479, 735, *et seq.*

[2] KÖLLIKER, *Éléments d'histologie humaine*, Paris, 1868, p. 723.

According to Luschka, as a rule, it is only the mucous membrane of the upper half of the body and the fundus of the uterus which is provided with ciliated epithelium, the movement being toward the openings of the Fallopian tubes. (LUSCHKA, *Anatomie des Menschen*, Tübingen, 1864, Bd. ii., S. 370.)

of the membrane in health, is grayish, viscid, and feebly alkaline. The tubes themselves have exceedingly thin, structureless walls, and are lined with cylindrical ciliated epithelial cells. These cells have been accurately described by Lott, who observed ciliary movement, as far down as their blind extremities, in some of the mammalia, the movement always being toward the openings.[1]

The changes which the mucous membrane of the body of the uterus undergoes during menstruation are remarkable. Under ordinary conditions, its thickness is from $\frac{1}{25}$ to $\frac{1}{14}$ of an inch; but it measures, during the menstrual period, from $\frac{1}{6}$ to $\frac{1}{4}$ of an inch.

In the cervix, the mucous membrane is paler, firmer, and thicker than over the body of the uterus, and presents a distinct line of demarkation. It is here more loosely attached to the subjacent tissue, and the anterior and posterior surfaces of the neck present an appearance of folds radiating from the median line, forming what has been called the arbor vitæ uteri, or plicæ palmatæ. These so-called folds are supposed by some anatomists to be formed by rows of large, papillary elevations of the membrane. Throughout the entire cervical membrane, are numerous mucous glands, and, in addition, in the lower portion, are a few rounded, semitransparent, closed follicles, called the ovules of Naboth, which are probably cystic enlargements of obstructed follicles. The upper half of the cervical membrane is smooth, but the lower half presents numerous villi.

According to the recent researches of Lott, who has elaborately investigated this subject and reviewed the opinions of previous writers, the epithelium of the cervix presents great variations in its character in different individuals. Before the time of puberty, Lott is of the opinion that the entire membrane of the cervix is covered with ciliated epithelium. After puberty, however, the epithelium of the lower portion

[1] LOTT, *Ueber das Flimmerepithel der Uterindrüsen*, in ROLLETT, *Untersuchungen*, Leipzig, 1871, Zweites Heft, S. 250, *et seq.*

changes its character, and we have cylindrical cells above, with squamous cells in the inferior portion. The latter extend upward in the neck to a variable distance.[1]

The blood-vessels of the uterus are very large, and present certain important peculiarities in their arrangement. The uterine arteries pass between the layers of the broad ligament to the neck, and then ascend by the sides of the uterus, presenting an exceedingly rich plexus of convoluted vessels, anastomosing above with branches from the ovarian arteries, sending branches over the body of the uterus, and finally penetrating the organ, to be distributed mainly in the middle layer of muscular fibres. In their course, these vessels present the convoluted arrangement characteristic of erectile tissue, and form a sort of mould of the body of the uterus. Rouget calls this the erectile tissue of the internal generative organs. By placing the pelvis in a bath of warm water, and injecting what he calls the spongy bodies of the ovaries and uterus by the ovarian veins, he produced a distention of the vessels and a true erection, the uterus executing a movement analogous to that of the penis during venereal excitement.[2]

In addition to the erectile action described by Rouget, Wernich has lately noted a true erection of the lower portion of the uterus, particularly the neck, which he believes to be very efficient in aiding the penetration of spermatozoids. In several observations, he noticed, during a vaginal examination by the touch, that the neck of the uterus, which at first was soft and flaccid, became elongated, hardened, and apparently in a condition of erection, giving an impression to the finger comparable to that of the hardened glans penis. As an anatomical explanation of the phenomena observed, Wernich quotes from Henle, an account of the arrangement of the blood-vessels of the cervix, and his physiological de-

[1] LOTT, *Zur Anatomie und Physiologie des Cervix Uteri*, Erlangen, 1872, S. 15, *et seq.*

[2] ROUGET, *op. cit.—Journal de la physiologie*, Paris, 1858, tome i., p. 338.

ductions from the presence, in this portion of the uterus, of a true erectile tissue.[1] This question will be considered more fully under the head of the mechanism of fecundation.

In the muscular structure of the uterus, are numerous large veins, the walls of which are closely adherent to the uterine tissue. During gestation, these vessels become enlarged, forming the so-called uterine sinuses.

Lymphatics are not very numerous in the unimpregnated uterus, but they become largely developed during gestation. They exist in a superficial and a deep layer, the deeper vessels coming from the muscular substance, and probably also from the mucous membrane.[2]

The uterine nerves are derived from the inferior hypogastric and the spermatic plexuses, and the third and fourth sacral. In the substance of the uterus, they present small collections of ganglionic cells, which were described by Dr. Robert Lee, in 1839.[3] According to Frankenhaeuser, they pass finally to the nucleoli of the muscular fibres.[4]

The Fallopian Tubes.—The Fallopian tubes, or oviducts, lead from the ovaries to the uterus. They are shown in Fig. 24, one being applied, by its fimbriated extremity, to the ovary. These tubes are from three to four inches long, but the length is not always equal upon the two sides. They lie between the folds of the broad ligament at its upper border. Opening into the uterus upon either side at the cornua, they present a small orifice, about $\frac{1}{25}$ of an inch in diameter. From the cornua, they take a somewhat undulatory course outward,

[1] WERNICH, *Ueber die Erectionsfähigkeit des unteren Uterusabschittes und ihre Bedeutung.—Beiträge zur Geburtshülfe und Gynäkologie*, Berlin, 1872, Bd. i., S. 296, *et seq.*

[2] A very elaborate article upon the lymphatics of the unimpregnated uterus has lately been published by Dr. Leopold, of Leipzig, which contains many new points of considerable anatomical interest. (LEOPOLD, *Die Lymphgefässe des normalen, nicht schwangeren Uterus.—Archiv für Gynaekologie*, Berlin, 1873, Bd. vi., S. 1, *et seq.*)

[3] LEE, *Memoir on the Ganglia and Nerves of the Uterus*, London, 1839.

[4] FRANKENHAEUSER, *Die Nerven der Gebaermutter*, Jena, 1867, S. 76, Taf. viii.

gradually increasing in size, so that they are rather trumpet-shaped. Near the ovary, they turn downward and backward. The extremity next the ovary is marked by from ten to fifteen fimbriæ, or fringes, which has given this the name of the fimbriated extremity, or morsus diaboli. All of these fringe-like processes are free, except one; and this one, which is longer than the others, is attached to the outer angle of the ovary, and presents a little gutter, or furrow, extending from the ovary to the opening of the tube. At this extremity, is the abdominal opening of the tube, which is two or three times as large as the uterine opening. Passing from the uterus, the caliber of the tube gradually increases as the tube itself enlarges, and there is an abrupt constriction at the abdominal opening.

Beneath the peritoneal coat, which is formed by the layers of the broad ligament, is a layer of connective tissue, containing a rich plexus of blood-vessels. This constitutes the proper fibrous coat of the Fallopian tubes.

The muscular layer is composed mainly of circular fibres, of the non-striated variety, with a few longitudinal fibres prolonged over the tube from the external muscular layer of the uterus. This coat is quite thick, and sends bands between the layers of the broad ligament to the ovary, which are supposed to act in adapting the fimbriated extremity of the tube to the surface of the ovary.

The mucous membrane of the tube is thrown into folds, which are longitudinal and transverse near the uterus, and are more complicated at the dilated portion. In this portion, next the ovary, embracing about the outer two-thirds, the folds project far into the caliber of the tube. These are sometimes simple, but more frequently they present secondary folds, often meeting as they project from opposite sides. This arrangement gives an arborescent appearance to the membrane on transverse section of the tube. The mucous membrane is covered by cylindrical ciliated epithelium, the movement of the cilia being from the ovary toward the uterus. At the

margins of the fimbriæ, the ciliated epithelium is continuous with the epithelium of the peritoneum, presenting the exceptional example of an opening of a mucous-lined tube into the cavity of the peritoneum. The membrane of the tubes has no mucous glands.

It is not necessary to enter into a minute description of the external organs of the female. Opening by the vulva, externally, and terminating at the neck of the uterus, is a membranous tube, the vagina. This lies between the bladder and the rectum; it is curved, being about four inches long in front, and five or six inches long posteriorly. There is a constricted portion at the outer opening, where we have a muscle, called the sphincter vaginæ, and the tube is somewhat narrowed at its upper end, where it embraces the cervix uteri. The inner surface presents a mucous membrane, marked by transverse rugæ, with papillæ and mucous glands. Its surface is covered with flattened epithelium. The vagina is quite extensible, as it must be during parturition, to allow the passage of the child. It presents a proper coat of dense fibrous tissue, with longitudinal and circular muscular fibres of the non-striated variety. We have, also, surrounding it, a rather loose erectile tissue, which is most prominent at its lower portion.

The parts composing the external organs are abundantly supplied with vessels and nerves. In the clitoris, which corresponds to the penis of the male, and on either side of the vestibule, we find a true erectile tissue.

CHAPTER XII.

THE OVUM AND OVULATION.

Structure of the ovum—Vitelline membrane—Vitellus—Germinal vesicle and germinal spot—Discharge of the ovum—Passage of ova into the Fallopian tubes—Puberty and menstruation—Description of a menstrual period—Characters of the menstrual flow—Changes in the uterine mucous membrane during menstruation—Changes in the Graafian follicle after its rupture (corpus luteum)—Corpus luteum of pregnancy.

We have now to study, as a necessary introduction to the history of development, the structure of the ripe ovum, the mechanism of its discharge from the Graafian follicle, and the phenomena which attend the process of ovulation.

Anterior to 1827, there was much discussion among physiologists, with regard to the production, discharge, etc., of the female element of generation. In 1827, Von Baer distinctly described the ovum in man and mammals, noted its relations to the Graafian follicle, concerning which there had been great confusion, and designated it as the veritable ovum, destined to be developed into the fœtus.[1] From this description, Von Baer is regarded as the discoverer of the human ovum; not so much because he was the first to see it, for imperfect descriptions of the ovum had been given, in rabbits, dogs, etc., many years before, but for the reason that his description was the most accurate, and settled several important points of dispute.

[1] De Baer, *Lettre sur la formation de l'œuf dans l'espèce humaine et dans les mammifères.—Publiée par* G. Breschet, Paris, 1829, p. 33. This letter was addressed to the Imperial Academy of Sciences of St. Petersburg, and was originally published at Leipzig, in 1827.

Structure of the Ovum.

The ripe ovum, as we have already indicated, lies in the Graafian follicle, embedded in the mass of cells which constitutes the discus proligerus. Within the discus, surrounding the ovum, there seem to be two kinds of cells; first, cells evidently belonging to the Graafian follicle, and similar to the cells in other parts of the membrana granulosa; second, a single layer of columnar cells, belonging to the ovum, and probably concerned in the production of the proper membrane of the ovum, the vitelline membrane. Regarding the vitelline membrane as the external covering, we can see, in the ovum, a clear, transparent membrane, a granular mass, the vitellus, filling this membrane completely, a large, clear nucleus, called the germinal vesicle, and a nucleolus, called the germinal spot.

The size of the ripe ovum, in the human subject and in mammals, is about $\frac{1}{120}$ of an inch, and its form is globular.

The external membrane is clear, apparently structureless, quite strong and resisting, and measures about $\frac{1}{2500}$ of an inch in thickness. As it forms a transparent ring in the mass of cells in which the ovum is embedded, this is sometimes called the zona pellucida. According to recent researches, it seems that the primordial ovum has at first no special investing membrane; as it develops, it presents, surrounding the vitellus, a single layer of columnar cells; at the deepest portion of these cells, a homogeneous basement membrane is gradually formed; and the cells undergo a sort of cuticular transformation, becoming finally the vitelline membrane.[1]

An important point, in this connection, is the question of the existence of pores, or perforations in the vitelline membrane. As we shall see farther on, there can be no doubt as to the actual penetration of the spermatozoids through this membrane, so that they come in contact with the vitellus; and it is

[1] WALDEYER, in STRICKER, *Manual of Human and Comparative Histology,* The New Sydenham Society, London, 1872, vol. ii., p. 177.

in this way that the ovum is fecundated. In the osseous fishes, there seems to be no question with regard to the existence of numerous pores in the vitelline membrane; but these are not so easily demonstrated in the ova of mammals. Many years ago, Barry described and figured a large opening, or micropyle, in the ovum of the rabbit, in which he thought he distinguished, on one occasion, a spermatozoid half-way through the membrane;[1] but this was probably an accidental rupture. A so-called micropyle has been described by Keber, in certain mollusks,[2] the existence of which is admitted by Coste, though he doubts the observation in which Keber described a spermatozoid, with the tail detached, in the act of penetrating the membrane. Coste himself states that the micropyle is seen with distinctness in the osseous fishes, as the salmon, trout, etc. "At the bottom of an umbilicus, visible with a simple loop, the vitelline membrane is pierced with a microscopic orifice, clearly defined, provided internally with a little valve."[3] Admitting the existence of a micropyle and pores in the vitelline membrane, in fishes and mollusks, it is certain that openings are very much more indistinct, if they can be seen at all, in the ova of mammals; still, the fact of the actual penetration of spermatozoids almost of necessity presupposes the presence of orifices. We have often thought, in studying this subject, that it must be difficult, examining a perfectly transparent and homogeneous membrane in water, which would fill up all pores, to distinguish any openings, and have been disposed to admit their presence, mainly because the spermatozoids are known to pass through. The idea of their existence in mammals certainly receives support from analogy with the lower orders of animals.

The vitellus, called the principal yolk or the formative

[1] BARRY, *Researches in Embryology.—Philosophical Transactions*, London, 1839, Part ii., p. 533.

[2] KEBER, *Ueber den Eintritt der Samenzellen in das Ei*, Königsberg, 1853, S. 18, *et seq.*

[3] COSTE, *Développement des corps organisés*, Paris, 1859, tome ii., p. 106.

yolk, contains the elements which are to undergo development into the embryon. It is composed of a semifluid mass, containing, in addition to the germinal vesicle, numerous granules. Some of these granules are large, strongly-refracting, globular bodies, which are so bright and so numerous, that they obscure the other parts of the vitellus. Between these, are numerous albuminoid granules, much smaller and not so distinct.

The germinal vesicle, sometimes called the vesicle of Purkinje,[1] is the enlarged nucleus of the primordial ovum.[2] It is a clear, globular vesicle, about $\frac{1}{550}$ of an inch in diameter, embedded in the vitellus, its position varying in different ova. It presents in its interior a number of fine granules, and a large, dark spot, called the germinal spot, or the spot of Wagner,[3] which measures about $\frac{1}{3600}$ of an inch in diameter. This spot corresponds to the nucleolus of the primordial ovum. In mammals, the mature ovum contains but one germinal vesicle and one germinal spot. The observation of Kölliker, who noted, as a rare exception, two vesicles in a human ovum, has not been confirmed.[4] The various points we have described are illustrated in Fig. 29.

[1] Purkinje (*Symbolæ ad Ovi Avium Historiam ante Incubationem*, Lipsiæ, 1830) was the first to describe this vesicle in the ova of birds. The original work of Purkinje was not regularly published until 1830, having been first presented, in 1825, at a reunion to celebrate the fiftieth anniversary of the doctorate of Blumenbach. Coste (*Développement des corps organisés*, Paris, 1847, tome i., p. 115, *et seq.*) discovered this vesicle in the mammalian ovum, his first publication bearing the date of 1834. In his large work, Coste seems to completely refute the claims of Bernhardt and of Wharton Jones to the discovery of the germinal vesicle in mammals.

[2] The ideas which have obtained within the last few years with regard to the development of mature ova from simple cells, called primordial ova, were advanced by Robin, as early as 1862. (ROBIN, *Mémoire sur les phénomènes qui se passent dans l'ovule avant la segmentation du vitellus.—Journal de la physiologie*, Paris, 1862, tome v., p. 67, *et seq.*)

[3] WAGNER, *Prodromus Historiæ Generationis Hominis atque Animalium*, Lipsiæ, 1836, p. 4.

[4] KÖLLIKER, *Éléments d'histologie humaine*, Paris, 1868, p. 705.

Discharge of the Ovum.

A ripe Graafian follicle measures from $\frac{3}{8}$ to $\frac{1}{2}$ an inch in diameter, and presents a rounded elevation, containing a plexus of blood-vessels, upon the surface of the ovary. At its most prominent portion, is an ovoid spot, in which the membranes are entirely free from blood-vessels. At this

FIG. 29.

Ovum of the rabbit, from a Graafian follicle $\frac{1}{12}$ of an inch in diameter.—*a*, epithelium of the ovum; *b*, zona pellucida, with radiating striations (vitelline membrane); *c*, germinal vesicle; *d*, germinal spot; *e*, vitellus. (WALDEYER, in STRICKER, *Handbuch der Lehre von den Geweben*, Leipzig, 1871, S. 555.)

spot, which is called the macula folliculi, the coverings finally give way, and the contents of the follicle are discharged. For a short time anterior to the rupture of the follicle, important changes have been going on in its structure. In the first place,

the non-vascular portion, situated at the very surface of the ovary, undergoes fatty degeneration, by which this part of the wall becomes gradually weakened. At the same time, at the other portions of the follicle, there is a growth of cells, which project into the interior, and an extension, into the interior, of blood-vessels in the form of loops. These processes, with an increase in the pressure of liquid and the fatty degeneration of the macula, cause the follicle to burst; and, with the liquid, the discus proligerus and the ovum are expelled. The formation of a cell-growth in the interior of the follicle is really the beginning of the corpus luteum; and this occurs some time before the discharge of the ovum takes place. It is a disputed question whether or not a hæmorrhage occurs into the follicle at the time of its rupture. This may, and undoubtedly does sometimes occur, but it cannot be regarded as constant, and has been denied by many observers.

The time at which the follicle ruptures, particularly with reference to the menstrual period, is probably not definite; but it is certain that, while sexual excitement may hasten the discharge of an ovum by producing a greater or less tendency to congestion of the internal organs, ovulation takes place independently of the act of coition. The opportunities for determining this fact in the human female are not frequent; but it has been fully demonstrated by observations upon the inferior animals, and there is now no doubt with regard to the identity of the phenomena of rut and of menstruation. It is useless, at the present day, to enter into an elaborate discussion of this point, which occupied so much the attention of the earlier writers. From the earliest times, it was recognized, not only that women became fruitful only after the appearance of the menses, but that sexual intercourse was most likely to be followed by conception when it occurred near the periods; a point which we shall discuss more fully under the head of fecundation. When it was recognized that rupture of Graafian follicles was followed by the formation of corpora lutea, it became easy to verify the supposition

that the ova were discharged at regular intervals, by an examination of the ovaries in women who had died suddenly; and such observations, showing corpora lutea in virgins, demonstrated that ovulation was not necessarily dependent upon coitus.[1]

Observations upon the lower animals have shown, notwithstanding the fact of discharge of ova without copulation or even the sight of the male, that sexual excitement has a certain influence upon ovulation. The experiments of Coste upon this point are very interesting. This observer noted that, in rabbits killed from ten to fifteen hours after copulation, there was evidence of the recent discharge of ova. In two experiments, however, he took female rabbits in heat and manifesting the greatest ardor for the male, presented them to the male, in order to show that they were really in heat, but carefully prevented copulation. This was done for three days in succession, there being, on each occasion, a manifest desire for the approach of the male. One rabbit was killed on the third day, while still in heat; and six distended Graafian follicles were found in one ovary and two in the other; but there was no trace of ruptured follicles. The other rabbit ceased to be in heat on the fourth day and was killed on the fifth. This animal presented seven distended follicles on one side, and one on the other, but no ruptured follicles.[2] From these and other experiments on the lower animals, there seems to be no doubt that copulation hastens the

[1] For numerous citations upon this point, the reader is referred to Coste (*Développement des corps organisés*, Paris, 1847, tome i., p. 195, *et seq.*). In 1837, Coste (*Embryogénie comparée*, Paris, 1837, tome i., p. 454) published an account of periodical ovulation in mammals occurring independently of copulation; but he admits that Négrier anticipated him, by several years, in a communication made to the *Société de médecine d'Angers*, in 1831, although this was not published until 1840. The observations of Négrier are all the more interesting, as they were made upon the human female. (Négrier, *Recherches anatomiques et physiologiques sur les ovaires dans l'espèce humaine*, Paris, 1840.) In the preface to this work, Négrier discusses the question of priority of his investigations.

[2] Coste, *Développement des corps organisés*, Paris, 1847, tome i., p. 183, *et seq.*

rupture of ripe Graafian follicles; but, on the other hand, it is equally true that follicles rupture independently of the sexual act. Bischoff, who first entertained the view that the contact of the spermatozoids with the ovary was necessary for the rupture of a follicle,[1] afterward actually discovered ova in the Fallopian tubes in sheep, bitches, sows, etc., during the rutting period, when copulation had been prevented.[2]

To return to the phenomena which attend ovulation in the human subject, there is every reason to suppose, at least from analogy, that the excitement of the genital organs during sexual intercourse may determine the rupture of a ripe Graafian follicle. At stated periods, marked by the phenomena of menstruation, one, and sometimes more Graafian follicles become distended and usually rupture and discharge their contents into the Fallopian tubes. This discharge of an ovum or ova may occur at the beginning, at the end, or at any time during the continuance of the menstrual flow. Upon this point, the observations of Coste, although they were made many years ago, seem entirely conclusive. In a woman who died on the first day of menstruation, he found a recently-ruptured follicle; in other instances, at a more advanced period and toward the decline of the menstrual flow, he found evidences that the rupture had occurred later; in the case of a female who drowned herself four or five days after the cessation of the menses, a follicle was found in the right ovary, so distended that it was ruptured by very slight pressure; and other instances were observed in which follicles were not ruptured during the menstrual period. The most striking case of this kind was of a young girl, nineteen years of age, who committed suicide fifteen days after the menstrual period. The ovaries were examined with the

[1] BISCHOFF, *Traité du développement de l'homme et des mammifères.—Encyclopédie anatomique*, Paris, 1863, tome viii., p. 21.

[2] BISCHOFF, *Sur la maturation et la chute périodique de l'œuf de l'homme et des mammifères, indépendamment de la fécondation.—Annales des sciences naturelles, Zoologie*, Paris, 1844, 3me série, tome ii., p. 124, *et seq.*

greatest care. "By the side of the Graafian vesicles largely developed, were found traces of ruptured vesicles; but the corpora lutea were evidently too old to be reasonably referred to the last menstruation; the Graafian vesicle, consequently, had not matured, or at least had been arrested in its development."

In conclusion, remembering that coitus may hasten the rupture of ripe follicles, we may quote the following as representing what we know of the relations between ovulation and menstruation:

"As a summary, then, of all the facts that I have observed, I believe it to be conclusive, that, in the human female, there is always, at each menstrual period, as during the condition of rut in mammals, a vesicle of the ovary which has a marked preponderance over the others; that it spontaneously arrives at maturity, and, most generally, is ruptured at some time during this period to give issue to the ovum which it contains; but there are cases, also, in which, in the absence of sufficiently favorable conditions, this distended vesicle cannot accomplish this end, and, as in mammals again, may remain stationary or be entirely reabsorbed."[1]

Passage of Ova into the Fallopian Tubes.

The fact that the ova, in the great majority of instances, pass into the Fallopian tubes, is sufficiently evident. The fact, also, that ova may fall into the cavity of the peritoneum is shown by the occasional occurrence of extra-uterine pregnancy, a rare accident, which shows that, in all probability, the failure of unimpregnated ova to enter the tubes is exceptional. When we come, however, to the mechanism of the passage of the ova into the tubes, the explanation is difficult.

At the present time, there are two theories; one, in which it is supposed that the fimbriated extremities of the tubes, at the time of rupture of the Graafian follicles, become adapted to the surface of the ovaries; and the other, that the

[1] COSTE, *Développement des corps organisés*, Paris, 1847, tome i., p. 222

ova are carried to the openings of the tubes by ciliary currents. Neither of these theories is capable of actual demonstration; and we can only judge of their probable correctness from anatomical facts. Rouget, an earnest advocate of the first-mentioned theory, has given an exact description of the muscular structures connected with the tubes and ovaries. We have already seen that one of the fimbriæ of the tube is longer than the others, and is attached to the outer angle of the ovary. The other fimbriæ are unattached, and are distant from about half an inch to an inch from the ovarian surface. According to this observer, there is a double layer of muscular fibres, passing from the lumbar region of the uterus and embracing the whole of the dilated portion of the tube; and the action of these fibres must draw the extremity of the tube toward the ovary and apply it to its surface.[1] That the muscular fibres described by Rouget exist, there can be scarcely a doubt; but that their action is essential to the passage of ova into the Fallopian tubes, is a question for discussion. If we could assume with certainty that the ova are discharged only during sexual intercourse, or that follicles are usually ruptured as a consequence of pressure exerted by the muscular action described by Rouget, this theory would be rendered exceedingly probable, to say the least; but the facts do not admit of this exclusive view. However, observations upon the lower animals, particularly rabbits, have shown that copulation actually hastens the discharge of ova from ripe Graafian follicles; but it must be a question of theory simply, whether the act be attended with the muscular contraction indicated by Rouget, or whether there be a determination of blood to the ovary, which produces an additional tendency to rupture at this time. We can hardly adopt unreservedly the theory of Rouget, unless it be evident that there is no other way in which the ova can enter the tubes. The

[1] ROUGET, *Recherches sur les organes érectiles de la femme, et sur l'appareil musculaire tubo-ovarien, dans leurs rapports avec l'ovulation et la menstruation.—Journal de la physiologie*, Paris, 1858, tome i., p. 748.

fact is that, in the human female, an ovum may be discharged at the beginning of menstruation, at any time during the flow, or even after the flow has ceased; and it is more than probable that pressure within the follicle alone may cause its rupture, and that this may occur independently of sexual excitement. In view of these facts, while we cannot deny that the fimbriated extremities of the tubes may, by muscular action, be approximated toward the surface of the ovary, we cannot admit that such an action is constant, or that it is necessary to the passage of ova into the tubes, though the theory of Rouget has been adopted, entirely or in part, by some writers of authority.[1]

If we take into account the situation of the ovaries and the relations of the Fallopian tubes, we can understand how an ovum may pass into the tube, without invoking the aid of muscular action. Let us suppose, for example, that a Graafian follicle be ruptured when the fimbriated extremity of the tube is not applied to the surface of the ovary. One of the fimbriæ, longer than the others, is attached to the outer angle of the ovary, and presents a little furrow, or gutter, leading to the opening of the tube. This furrow is lined by ciliated epithelium, as indeed, is the mucous membrane of all of the fimbriæ, the movements of which produce a current in the direction of the opening, which we might suppose would be sufficient to carry a little globule, only $\frac{1}{120}$ of an inch in diameter, into the tube. At the same time, there is probably, as has been suggested by Becker,[2] a constant flow of liquid over the ovarian surface, directed by the ciliary current toward the tube; and when the liquid of the ruptured follicle is discharged, this, with the ovum, takes the same course.

In all probability, what we have just described is the mechanism of the passage of the ova into the Fallopian

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 828; KÖLLIKER, *Éléments d'histologie humaine*, Paris, 1868, p. 716.

[2] BECKER, *Ueber Flimmerepithelium und Flimmerbewegung im Geschlechtsapparate der Säugethiere und des Menschen.—Untersuchungen zur Naturlehre des Menschen und der Thiere*, Frankfurt a. M., 1857, Bd. ii., S. 92.

tubes; and it is possible that the fimbriated extremity may be drawn toward the ovarian surface, though we can hardly understand how it can be closely applied to the ovary and exert any considerable pressure upon the distended follicle. It is proper to note, also, that the conditions dependent upon the currents of liquid directed by the movements of cilia are constant, and could influence the passage of an ovum at whatever time it might be discharged, while a muscular action would be more or less intermittent.

It is somewhat difficult to understand the exact mechanism of the passage of an ovum discharged from an ovary into the Fallopian tube upon the opposite side, although it cannot be doubted that this sometimes occurs. Schroeder has collected, from various authors, the reports of several cases, in which an ovum has been discharged, has found its way into the uterus, and has undergone development, one tube being closed and the corpus luteum existing upon the side on which the tube was impervious. In some instances in which the corpus luteum has been found on the side on which the tube was closed, tubal pregnancy has occurred upon the opposite side.[1] In these cases, the ovum must have passed across the uterus. It is possible that, the subject lying upon one side, a current of liquid may have taken a direction from the ovary to the opposite tube, but this can be only a mere supposition.

Puberty and Menstruation.

At a certain period of life, usually between the age of thirteen and of fifteen years, the human female undergoes a remarkable change and arrives at what is termed the age of puberty. At this time, there is a marked increase in the general development of the body; the limbs become fuller and more rounded; a growth of hair makes its appearance upon the mons veneris; the mammary glands increase in size

[1] SCHROEDER, *Lehrbuch der Geburtshülfe*, Bonn, 1871, S. 19.

and take on a new stage of development;[1] Graafian follicles enlarge, and one or more approach the condition favorable to rupture and the discharge of ova. At this time, also, certain changes are observed in the moral, as well as in the physical attributes of the female. There is then a sort of indefinite consciousness of a capacity for new functions, with an indescribable change in feeling for the opposite sex, due to the first development of sexual instincts. The female becomes capable of impregnation, and continues so, in the absence of pathological conditions, until the cessation of the menses.

It is a commonly-recognized fact that the age of puberty is earlier in warm than in cold climates; and numerous instances are on record, in which the menses have appeared exceptionally, much before the usual period. Generally, at the age of forty or forty-five, the menstrual flow becomes irregular; it occasionally loses its sanguineous character, and it usually ceases at about the age of fifty years. Sometimes it is said that the menses return, with a second period of fecundity, though this is rare.[2] According to most writers, while climate has a certain influence over the time of cessation as well as the first appearance of the menses, this is not very marked. When the menses appear early in life, they usually cease at a correspondingly early period; but this is by no means constant. There are, also, numerous exceptions to the ordinary limits to the period of fecundity. Haller observed a case of a young girl, nine years of age, who had menstruated for several years, and others, who had become pregnant at nine, ten, and twelve years. He also quotes cases of women who have been fruitful at from fifty-four to seventy years of age.[3] Other instances of this kind are on record,[4] which it is un-

[1] For an account of the changes in the mammary glands at puberty, see vol. iii., Secretion, p. 75.

[2] Cases of this kind were noted by Haller. (*Elementa Physiologiæ*, Bernæ, 1765, tomus vii., pars ii., p. 141.)

[3] HALLER, *op. cit.*, pp. 139, 142.

[4] In a recent publication, several interesting examples are given of early menstruation and conception. (HARRIS, *Early Pregnancy.—American Journal of*

necessary to quote. The occurrence of pregnancy after the age of fifty or fifty-five is certainly doubtful.

Menstruation.

It is unnecessary to discuss farther the correspondence between menstruation in the human female and the condition of heat in the lower animals, as we have already seen, under the head of ovulation, that these two conditions are essentially identical. In the lower animals, the female will admit the male only at the period of heat; and in some animals in the savage state, it is only at this time that the male is capable of copulation. The variations in sexual temperament in the human female are so considerable, and the sentiments toward the opposite sex are so subordinate to artificial conditions of society and civilization, that it is difficult to establish a parallel, in this regard, between her and the lower animals. Some females rarely or never experience sexual excitement and have no orgasm during intercourse; while others are capable of sexual ardor at any time. Women who are in the habit of promiscuous relations with the other sex frequently lose the sexual feeling and simulate excitement during coitus. It is very difficult, indeed, to say positively how far the facts observed in the lower animals are applicable to the human subject, as we must depend largely upon statements which, of themselves, are entitled to but little consideration. It is nevertheless true that, in some women, sexual desire is decidedly marked just after the cessation of the menses, and in many, it really exists at no other time. Still, mercenary or other considerations may induce women to admit intercourse at any time, and the sexual orgasm, and even fecundation, may at any time occur. As a rule, the female yields to advances made by the male, and is reputed to experience a less degree of sexual desire and ardor, though this has marked exceptions. It is probably true that, eliminating, as

Obstetrics, New York, 1874, vol. vi., p. 571, *et seq.*; and, *Transactions of the Philadelphia Obstetrical Society.*—Ibid., p. 637, *et seq.*)

far as we can, all considerations except those of a purely sexual character, there is less of a promiscuous feeling for the opposite sex in females than in males, and that sexual desire, aside from feelings of fatigue or satiety, is sometimes markedly periodical in women. If we may take certain individual cases as representing physiological conditions, it appears that, in some women, there is a period of comparative indifference to the opposite sex; as the menses approach, there is more or less irritability of temper and disinclination for society, which disappear as the flow is established; and at or following the cessation of the menses, sexual desire is manifested to an unusual degree, this continuing for only a few days.

Although there is a periodical condition of heat in the lower animals, connected with ovulation, a sanguineous discharge from the genital organs is not often observed. It is only in monkeys that we have a counterpart of what occurs in the human female; and observations upon these animals have shown that they are subject to a monthly discharge of blood, at this time giving evidence of unusual salacity.[1]

In the human female, near the time of puberty, there is sometimes a periodical sero-mucous discharge from the genital organs, preceding, for a few months, the regular establishment of the menstrual flow. Sometimes, also, after the first discharge of blood, the female passes several months without another period, when the second flow takes place, and the menses then become regular. In a condition of health, the periods recur every month, until they cease, at what is termed the change of life. In the majority of cases, the flow recurs on the twenty-seventh or the twenty-eighth day; but sometimes the interval is thirty days. As a rule, also, utero-gestation, lactation, and most severe diseases, acute and chronic, suspend the periods; but this has exceptions, as some females menstruate regularly during pregnancy, and

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 765; COSTE, *Développement des corps organisés*, Paris, 1847, tome i., pp. 188, 228.

it is not very uncommon for the menses to appear during lactation.

As we should naturally expect, from the connection between menstruation and ovulation, removal of the ovaries, especially when this occurs before the age of puberty, usually produces arrest of the menses. It is a well-known fact that animals do not present the phenomena of heat after extirpation of the ovaries. Raciborski has quoted cases of this operation in the human subject, in which the menses were arrested;[1] but this rule does not appear to be absolute, as Dr. H. R. Storer reports at least one case, in which menstruation continued with regularity for more than a year after removal of both ovaries.[2] When a cow brings forth twins, one a male and the other apparently a female, the latter is called a free-martin, and generally has no ovaries. Hunter, in his paper on the free-martin, gives a full description of this anomalous animal, and states that it does not breed or show any inclination for the bull.[3] In 1868, we had an opportunity of examining the generative organs of a free-martin.

[1] RACIBORSKI, *De la puberté*, Paris, 1844, p. 100.

[2] STORER, *De la menstruation sans ovaires.—Archives de physiologie*, Paris, 1868, tome i., p. 376. Other cases of this kind are on record.

As these pages are going through the press, we have received, from Prof. T. G. Thomas, the following very interesting account of five operations in which both ovaries were removed:

"In reply to your note of to-day, I would state that I have extirpated both ovaries in menstruating women five times, with the following results:

"*Case* 1.—(Heard from two years and eleven months after the operation.) No symptoms of menstruation.

"*Case* 2.—(Heard from two and a half years after the operation.) No symptoms whatever of menstruation.

"*Case* 3.—(Not heard from.)

"*Case* 4.—(Heard from nearly six months after the operation.) Up to the present time this patient has manifested no symptoms whatever of menstruation, but now states that she has a bloody discharge from the vagina and all the symptoms accompanying the menstrual function.

"*Case* 5.—(Heard from five and a half months after the operation). No symptoms whatever of menstruation."

[3] HUNTER, *Account of the Free Martin.—Observations on certain Parts of the Animal Œconomy*, London, 1792, p. 60.

raised and killed by Prof. James R. Wood. In this animal, the uterus was rudimentary and there were no ovaries.

A menstrual period usually presents three stages: first, invasion; second, a sanguineous discharge; third, cessation.

The stage of invasion is variable in different females. There is usually, anterior to the establishment of the flow, more or less of a feeling of general *malaise*, a sense of fulness and weight in the pelvic organs, accompanied with a greater or less increase in the quantity of vaginal mucus, which becomes brownish or rusty in color. It is probable that, at this time, the discharge has a peculiar odor, though this point is somewhat difficult to determine. In the lower animals, at least, there is certainly a characteristic odor during the rutting period, which attracts the male. At this time, also, the breasts become slightly enlarged, showing the connection between these organs and the organs of generation. This stage may continue for one or two days, although, in many instances, the first evidence of the access of a period is a discharge of blood.

When the general symptoms above indicated occur, the sense of uneasiness is usually relieved by the discharge of blood. During this, the second stage, blood flows from the vagina in variable quantity, and the discharge continues for from three to five days. With regard to the duration of the flow, there are great variations in different individuals. Some women present a flow of blood for only one or two days; while, in others, the flow continues for from five to eight days, within the limits of health. A fair average, perhaps, is four days.[1] It is also difficult to arrive at an approximation, even, of the total quantity of the menstrual flow. Burdach estimated it at from five to six ounces.[2] According

[1] Burdach makes the following statement with regard to certain conditions capable of modifying the menstrual flow: "The flow is more abundant in the indolent than in women accustomed to labor; in those of feeble constitution than in those who enjoy robust heath; in inhabitants of cities than in inhabitants of villages." (*Traité de physiologie*, Paris, 1837, tome i., p. 288.)

[2] BURDACH, *op. cit.*, p. 286.

to Longet, this estimate is rather low, the quantity ordinarily ranging from ten to twelves ounces, occasionally amounting to seventeen ounces, or even more.[1] It is well known that the quantity is exceedingly variable, as is the duration of the flow, and the difficulties in the way of collecting and estimating the total discharge are evident.

The characters of the menstrual flow are sufficiently simple. Supposing the discharge to continue for four days, on the first day, the quantity is comparatively small; on the second and third, the flow is at its height; and the quantity is diminished on the fourth day. During this stage, the fluid has the appearance of pure arterial blood, not coagulated, and mixed, as has been shown by microscopical examination, with pavement-epithelium from the vagina, cylindrical cells from the uterus, leucocytes, and a certain amount of sero-mucous secretion. Chemical examination of the fluid does not show any marked peculiarities, except that the quantity of fibrin is either not estimated or is given as much less than in ordinary blood.[2]

The mechanism of the hæmorrhage, which will be considered more fully when we come to study the changes in the uterine mucous membrane during menstruation, is probably the same as in epistaxis. There is a rupture of small blood-vessels, probably capillaries, and blood is thus exuded from the entire surface of the membrane lining the uterus, and sometimes from the membrane of the Fallopian tubes. The blood is then discharged into the vagina and is kept fluid by the vaginal mucus. The mucus of the body of the uterus is viscid and alkaline; the mucus secreted at the neck is gelatinous, viscid, tenacious, and also alkaline; the

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 772.

[2] Several analyses of the menstrual fluid, taken from the older writers, are given by Simon. (*Animal Chemistry*, Philadelphia, 1846, p. 274.) According to more recent observations, the menstrual blood is only apparently deficient in fibrin, because coagulation is prevented by admixture with vaginal mucus. (GORUP-BESANEZ, *Lehrbuch der physiologischen Chemie*, Braunschweig, 1862, S. 333.)

vaginal mucus is decidedly acid, creamy, and not viscid, containing numerous cells of scaly epithelium, and leucocytes.

The third stage, that of cessation of the menses, is very simple. During the latter part of the second stage, the flow of blood gradually diminishes; the discharge becomes rusty, then lighter in color; and, in the course of about twenty-four hours, it assumes the characters observed in the intermenstrual period.

When the menstrual flow has been established, there is no very marked general disturbance, except a sense of lassitude, which may become exaggerated if the discharge be unusually abundant. It has been noted, however, by Rabuteau, that, during the menstrual period, the production of urea is diminished more than twenty per cent., that the pulse becomes slower, and that the temperature falls at least one degree (half a degree, centigrade).[1]

Changes in the Uterine Mucous Membrane during Menstruation.—If the mucous membrane of the uterus be examined during the menstrual flow, it is found smeared with blood, which sometimes extends into the Fallopian tubes. It is then much thicker and softer than during the intermenstrual period. Instead of measuring about $\frac{1}{14}$ of an inch in thickness, as it does under ordinary conditions, its thickness is from $\frac{1}{8}$ to $\frac{1}{4}$ of an inch. It becomes more loosely attached to the subjacent parts, is somewhat rugous, and the glands are very much enlarged. At the same time, there are developed, in the substance of the membrane, numerous spherical and fusiform cells.[2] According to the recent and very striking researches of Kundrat and Engelmann, this condition probably precedes the discharge of blood by several days; during which time, the membrane is gradually preparing for the reception of the ovum. One of the most important points in these researches is that there is a fatty degeneration of the

[1] RABUTEAU, *De l'influence de la menstruation sur la nutrition.—Gazette hebdomadaire*, Paris, 1870, 2me série, tome vii., p. 402.

[2] KÖLLIKER, *Éléments d'histologie humaine*, Paris, 1868, p. 726.

different elements entering into the structure of the mucous membrane, including the blood-vessels, this change being most marked at the surface; and it is on account of the weakened condition of the vascular walls that the hæmorrhage takes place. A short time after the flow has ceased, the mucous membrane returns to its ordinary condition.[1]

We have already noted that there is a considerable desquamation of epithelium from the uterus with the flow of blood, during the menstrual period. Sometimes, in normal menstruation, the epithelium is in the form of patches; and, in certain cases of dysmenorrhea, there is a membranous exfoliation, which has led to the idea that the mucous membrane is actually thrown off. In normal menstruation, there is no true exfoliation of the membrane, and, even in what is called membranous dysmenorrhea, the so-called membrane is usually nothing more than a membraniform exudation, secreted by the mucous surface.

Changes in the Graafian Follicles after their Rupture (Corpus Luteum).—After the discharge of an ovum, the Graafian follicle undergoes certain retrograde changes, involving the formation of what is called the corpus luteum. Even when the discharged ovum has not been fecundated, the corpus luteum persists for several weeks, so that, ovulation occurring every month, several of these bodies, in various stages of retrogression, may sometimes be seen in the ovaries. Corpora lutea were observed by some of the earliest writers upon anatomy; but the first description presenting any ap-

[1] KUNDRAT UND ENGELMANN, *Untersuchungen über die Uterusschleimhaut.—Medicinische Jahrbücher*, Wien, 1873, S. 135, *et seq.*

The researches embodied in the above paper are of great importance in their bearing upon the physiology of menstruation, the preparation of the mucous membrane of the uterus for the reception of the fecundated ovum, and calculations of the duration of pregnancy. From the facts and arguments brought forward, there can be scarcely a doubt that the flow of blood is mainly due to fatty degeneration of the most superficial portion of the mucous membrane. The points in these observations which relate to the question of the preparation of the uterus for the reception of the ovum will be considered hereafter.

proach to accuracy was given by De Graaf.[1] After De Graaf, Malpighi described these bodies, and was the first to apply to them the name of corpora lutea.[2] The older writers, however, had no very clear ideas regarding the formation of the corpora lutea, and it is only since we have become familiar with the mechanism of ovulation, that we have been able to comprehend their physiological significance.

For a certain time anterior to the discharge of the ovum, there is a cell-growth from the proper coat of the Graafian follicle, and probably from the membrana granulosa, with a projection of looped blood-vessels into the interior of the follicle, which is the first formation of the corpus luteum. At the time of rupture of the follicle, the ovum, with a great part of the membrana granulosa, is discharged. Sometimes, at the time of rupture of the follicle, there is a discharge of blood into its interior; but this is not constant, though we usually have a gelatinous exudation, more or less colored with blood. At the same time, the follicular wall undergoes hypertrophy, becomes convoluted, or folded, and highly vascular. This convoluted wall, formed by the proper coat of the follicle, is surrounded by the fibrous tunic, and its thickening is most marked at the deepest portion of the follicle. At the end of about three weeks, the body, which is now called the corpus luteum, on account of its yellowish or reddish-yellow color, has arrived at the height of its development, and measures about half an inch in depth by about three-quarters of an inch in length, its form being ovoid.[3] The convoluted wall then contains a layer of large, pale, finely-granular cells, which are internal, and are supposed to be the remains of the epithelium of the follicle. The great mass of this wall, however, is composed of large nucleated cells, containing fatty globules and granules of reddish or

[1] De Graaf, *De Mulierum Organis Generationi inservientibus*, Lugd. Batav., 1672, p. 178.

[2] Malpighius, *Opera omnia*, Lond., 1687, tomus i., Appendix, 1686, pp. 30, 31.

[3] Dalton, *Human Physiology*, Philadelphia, 1871, p. 598.

yellowish pigmentary matter. The thickness of the wall is about one-eighth of an inch, at its deepest portion.

After about the third week, the corpus luteum begins to retract; its central portion and the convoluted wall become paler, and, at the end of seven or eight weeks, a small cicatrix marks the point of rupture of the follicle.

The above are the changes which occur in the Graafian follicles after their rupture and the discharge of ova, when the ova have not been fecundated; and the bodies thus produced are called false corpora lutea, as distinguished from corpora luteà found after conception, which are called true corpora lutea.

Corpus Luteum of Pregnancy.—Before the process of spontaneous ovulation and its connection with menstruation were understood, anatomists were unable to make a definite distinction between the corpus luteum following the discharge of an ovum without fecundation, called the corpus luteum of menstruation, and the corpus luteum of pregnancy. Huschke, however, as early as 1845, recognized the distinction between the false and the true corpora lutea. He states that, "after fecundation they develop in a more rapid manner, and assume the form of true corpora lutea;" and farther, he says that "corpora lutea are also produced, without fecundation, to which the name false has been given."[1] Notwithstanding that the so-called true and false corpora lutea seem to have been well recognized, even by writers anterior to Huschke,[2] it remained for Coste to exactly describe the various points of distinction between them; and his account of the differences in the development of these bodies, dependent upon the non-fecundation or the fecundation of the

[1] HUSCHKE, *Traité de splanchnologie.—Encyclopédie anatomique*, Paris, 1845, tome v., p. 427.

[2] Bischoff, as well as other writers of his time, frequently referred to true and false corpora lutea. (*Observations sur le détachement et la fécondation de l'œuf humain et des œufs des mammifères.—Annales des sciences naturelles, Zoologie*, Paris, 1848, seconde série, tome xx., p. 93, *et seq.*)

ovum, is still regarded as entirely accurate, and answers the requirements of science at the present day, even in its medico-legal aspects, as well as in 1847, when his observations were published.[1]

When a discharged ovum has been fecundated, the corpus luteum passes through its various stages of development and retrogression much more slowly than the ordinary corpus luteum of menstruation. It is then called, to distinguish it from the latter, the true corpus luteum. We cannot do better than to quote, in the words of Coste, the description of the changes which this body undergoes in pregnancy:

"I have followed, with the greatest care, in the pregnant female, all the phases of this retrogression. This commences to be really appreciable toward the end of the third month. During the fourth month, the corpus luteum diminishes by nearly a third, and toward the end of the fifth, it is ordinarily reduced one-half. It still forms, however, during the first days after parturition, and in the greatest number of cases, a tubercle which has a diameter of not less than from $\frac{2}{5}$ to $\frac{1}{3}$ of an inch. The tubercle afterward diminishes quite rapidly; but it is nearly a month before it is reduced to the condition of a little, hardened nucleus, which persists more or less as the last vestige of a process so slow in arriving at its final term. Nevertheless, there is nothing absolute in the retrograde progress of this phenomenon. I have seen women, dead at the sixth and even the eighth month of pregnancy, present corpora lutea as voluminous as others at the fourth month.

"Though it may not be, in general, that, after parturition,

[1] Dr. Robert Knox published, in 1844, a table of measurements of the corpus luteum at various stages of gestation, two of the observations being his own, and the others, taken from different authors. Dr. Knox mentioned true and false corpora lutea, but evidently had no distinct idea of their differences. His article seems to be intended to show that the paper on the same subject, by Sir Everard Home, was composed of inexact statements borrowed from the unpublished writings of John Hunter. (KNOX, *Contributions to Anatomy and Physiology. On the Corpus Luteum.—The London Medical Gazette*, 1844, New Series, vol. i., p. 605.)

the corpora lutea disappear, it is nevertheless not without examples that they disappear much more promptly. I have had the opportunity of examining the body of a woman, dead in the course of the eighth month of pregnancy, in whom the absorption was already complete. Facts of this kind are doubtless very rare, as only one has occurred in my observations, notwithstanding the numerous researches to which I have devoted myself for a long time. . . .

"There exists a notable difference between the corpora lutea which are formed as the sequence of conception, and those which occur aside from the conditions developed by impregnation. The duration of the former is much longer than that of the latter, and the volume becomes, also, much more considerable, although their nature is, in truth, identical. I have too often had occasion to remark this, in the ovaries of suicides, to retain the slightest doubt in this regard."[1]

		CORPORA LUTEA.		OBSERVATIONS.
		Long diameter.	Short diameter.	
Stages of pregnancy.	25 to 30 days.....	3/4 inch.	1/2 inch.	It is rare that a corpus luteum assumes a spherical form, and that, whatever be the section, its diameters are equal, or nearly so. It generally undergoes, in its development, a sort of compression in the same way as does the ovary. Here, only the long and the short diameters, taken from a section of the corpora lutea, have been measured, the ovary being divided longitudinally, and, as it is, generally figured in the plates of the atlas.
	About 40 days....	1 "	3/5 "	
	2 months.........	1 "	3/5 "	
	3 months.........	1 "	3/4 "	
	In the 4th month..	3/5 "	3/5 "	
	Idem...........	1/2 "	2/5 "	
	Idem...........	1/2 "	2/5 "	
	In the 5th month..	3/5 "	2/5 "	
	5 months.........	1/2 "	1/2 "	
	In the 6th month..	1/2 "	1/2 "	
	7 months.........	3/5 "	1/4 "	
	In the 9th month...	3/5 "	2/5 "	
After parturition.	20 hours after.....	3/5 "	7/25 "	
	8 days after....	3/5 "	1/3 "	Double gestation.
		1/5 "	7/25 "	
	Idem..........	3/5 "	1/4 "	Double gestation.
		3/5 "	1/4 "	
	7 days after.......	3/5 "	1/5 "	

The preceding table, also quoted from Coste (*op. cit.*, p. 256), shows the different stages of the corpus luteum of preg-

[1] Coste, *Développement des corps organisés*, Paris, 1847, tome i., pp. 254, 257.

nancy. It will be remembered that the corpus luteum of menstruation is at its maximum of development at the end of about three weeks, when it measures half an inch in depth by three-quarters of an inch in length; that it then begins to retract, and becomes a small cicatrix at the end of seven or eight weeks.

In 1851, Dr. J. C. Dalton published an essay on the "Corpus Luteum of Menstruation and Pregnancy," in which he pointed out very accurately the different points of distinction between what had been known as the false and the true corpora lutea. These observations it is unnecessary to quote in detail, as the results were almost identical with those obtained by Coste; but they are peculiarly interesting, not only from the accuracy of the descriptions, but as they were made independently, and without any knowledge of the publication by Coste, four years before.[1]

[1] DALTON, *Prize Essay on the Corpus Luteum of Menstruation and Pregnancy.—Transactions of the American Medical Association*, Philadelphia, 1851, vol. iv., p. 547, *et seq.*

In a note appended to this essay, Dr. Dalton refers to Longet's Physiology (Paris, 1850), in which the distinction between the two varieties of corpora lutea is made; but his own investigations, which are remarkable for their completeness and accuracy, were made independently and without any knowledge of the observations by Coste. Dr. Dalton's researches on this subject have been extensively quoted, have done much to settle the important question of the exact distinctions between the corpora lutea of menstruation and of pregnancy, and at once established his reputation as an accurate and trustworthy observer. The views of Coste were then almost unknown in this country.

CHAPTER XIII.

MALE ORGANS AND ELEMENTS OF GENERATION.

The testicles—Tunica vaginalis—Tunica albuginea—Tunica vasculosa—Seminiferous tubes—Epididymis—Vas deferens—Vesiculæ seminales—Prostate—Glands of the urethra—Semen—Secretions mixed with the products of the testicles—Spermatozoids—Development of the spermatozoids—Seminal fluid in advanced age.

There is not the same physiological interest attached to the anatomical study of the male genitalia, particularly the external organs, as there is to the corresponding parts in the female, for the reason that the function of the spermatozoids is accomplished within the female organs, where they unite with the ovum and where the processes of development take place. The anatomy of the penis and urethra has a more exclusively surgical interest. As physiologists, we have to study the testicles, organs which correspond to the ovaries, and in which the male generative element is developed, the various glandular structures which secrete fluids forming a part of the ejaculated semen, the mechanism of erection, by which penetration of the male organ into the vagina is rendered possible, the composition of the seminal fluid and the mechanism of its ejaculation, and the course of the semen in the generative passages of the female, until it is brought in contact with and fecundates the ovum. As regards the penis, it will be sufficient to describe, as we shall under the head of coitus, the mechanism of erection and of the ejaculation of semen. It will be necessary, however, to study the structure of the testicles and of the various glandular organs connected with the urethra, in order to understand the development of the spermatozoids and the composition of the seminal fluid.

The Testicles.

The testicles are two symmetrical organs, situated, during a certain portion of intra-uterine life, in the abdominal cavity, but finally descending into the scrotum. Within the scrotum, which is a pouch-like process of integument, are the two testicles, with their coverings, vessels, nerves, etc. The skin of the scrotum encloses both testicles, but is marked by a median raphe. Immediately beneath the skin, is a loose, reddish, contractile tissue, called the dartos, which forms two distinct sacs, one enveloping each testicle, the inner portion of these sacs fusing in the median line, to form the septum. Within these two sacs, the coverings of each testicle are distinct. These organs are, as it were, suspended in the scrotum by the spermatic cords, the left usually hanging a little lower than the right. The coverings for each testicle, in addition to those just mentioned, are the intercolumnar fascia, the cremaster muscle, the infundibuliform fascia, the tunica vaginalis, and the proper fibrous coat.

The tunica vaginalis is a shut sac of serous membrane, covering the testicle and epididymis, and reflected from the posterior border of the testicle to the wall of the scrotum, lining the cavity occupied by the testicle on either side, and also extending over the spermatic cord. This tunic is really a process of peritoneum, which has become shut off from the general lining of the abdominal cavity. The spermatic cord is composed of the vas deferens, blood-vessels, lymphatics, and nerves, with the various coverings already described, which expand and surround the testicle.

Beneath the tunica vaginalis, are the testicles, with their proper fibrous coat. These organs are ovoid, and flattened laterally and posteriorly. "They are from an inch and a half to two inches long, about an inch and a quarter from the anterior to the posterior border, and nearly an inch from side to side. The weight of each varies from three-quarters of an ounce to an ounce, and the left is often a little the

larger of the two."[1] The proper fibrous coat is everywhere covered by the closely-adherent tunica vaginalis, except at the posterior border, where the vessels enter and the duct passes out. At the outer edge of this border, is the epididymis, formed of convoluted tubes, presenting a superior enlargement, called the globus major, a long mass running the length of the testicle, called the body, and a smaller enlargement inferiorly, called the globus minor. This, too, is covered with the tunica vaginalis. Between the membrane covering the testicle and epididymis and the layer lining the scrotal cavity, is a small quantity of serum, just enough to moisten the serous surfaces. At the superior portion of the testicle, we usually find one or more small, ovoid bodies, attached to the testicle by short, constricted processes, which are called the hydatids of Morgagni. These have no physiological importance, and are supposed to be the remains of fœtal structures.

The proper fibrous coat of the testicle is called the tunica albuginea. It is white, dense, inelastic, measures about $\frac{1}{25}$ of an inch in thickness, and is simply for the protection of the contained structures. Sections of the testicle, made in various directions, show an incomplete vertical process of the tunica albuginea, called the corpus Highmorianum, or the mediastinum testis. This is wedge-shaped, about $\frac{1}{8}$ of an inch wide at its superior and thickest portion, is pierced by numerous openings, and lodges blood-vessels and seminiferous tubes. From the mediastinum, numerous delicate, radiating processes of connective tissue pass to the inner surface of the tunica albuginea, dividing the substance of the testicle into imperfect lobules, which lodge the seminiferous tubes. Luschka estimates the number of these lobules at from one hundred and fifty to two hundred.[2] Their shape is pyrami-

[1] QUAIN, *Elements of Anatomy*, London, 1867, vol. ii., p. 967. For the sake of uniformity of description, most of the measurements of the different parts of the testicle will be taken from the above work.

[2] LUSCHKA, *Anatomie des Menschen*, Tübingen, 1864, Bd. ii., S. 267.

dal, the larger extremities presenting toward the surface, and the pointed extremities situated at the mediastinum.

Lining the tunica albuginea and following the mediastinum and the processes which penetrate the testicle, is a tunic, composed of blood-vessels and delicate connective tissue, called the tunica vasculosa.

Lodged in the cavities formed by the trabeculæ of connective tissue, are the seminiferous tubes, in which the male elements of generation are developed. These tubes exist to the number of about eight hundred and forty in each testicle, and constitute almost the entire substance of the lobules. The larger lobules contain five or six tubes, the lobules of medium size, three or four, and the smallest frequently enclose but a single tube.[1] Each tube presents a convoluted mass, which can frequently be disentangled under water, particularly if the testicle be macerated for several months in water with a little nitric acid. The entire length of the tube, when thus unravelled, is about thirty inches, and its diameter is from $\frac{1}{200}$ to $\frac{1}{150}$ of an inch. It begins by from two to seven short, blind extremities and sometimes by anastomosing loops. The cæcal diverticula are found usually in the external half of the tube, and their length is from $\frac{1}{12}$ to $\frac{1}{8}$ of an inch. The anastomoses are sometimes between the tubes of different lobules, sometimes between tubes in the same lobule, and sometimes between different points in the same tube.[2] As the tubes pass toward the posterior portion of the testicle, they unite into about twenty straight canals, called the vasa recta, about $\frac{1}{75}$ of an inch in diameter, which penetrate the substance of the mediastinum testis. In the mediastinum, the tubes form a close net-work, called the rete testis; and, at the upper portion of the posterior border, they pass out of the testicle, by from twelve to fifteen openings, and are here called the vasa efferentia.

Having passed out of the testicle, the vasa efferentia form

[1] Sappey, *Traité d'anatomie*, Paris, 1874, tome iv., p. 601.

[2] Sappey, *loc. cit.*, p. 606.

a series of small, conical masses, which together constitute the globus major, or head of the epididymis. Each of these tubes, when unravelled, is from six to eight inches long, gradually increasing in diameter, until they all unite into a single, convoluted tube, which forms the body and the globus minor of the epididymis. This single tube of the epididymis, when unravelled, is about twenty feet in length.

FIG. 90.

Testicle and epididymis of the human subject. After Arnold.—*a*, testicle; *b*, lobules of the testicle; *c*, vasa recta; *d*, rete testis; *e*, vasa efferentia; *f*, cones of the globus major of the epididymis; *g*, epididymis; *h*, vas deferens; *i*, vas aberrans; *m*, branches of the spermatic artery to the testicle and epididymis; *n*, ramification of the artery upon the testicle and epididymis; *o*, deferential artery; *p*, anastomosis of the deferential with the spermatic artery. (KÖLLIKER, *Handbuch der Gewebelehre*, Leipzig, 1867, S. 528.)

The walls of the seminiferous tubes in the testicle itself are composed of connective tissue, a basement-membrane, and a lining of granular, nucleated cells. In the rete testis, it is uncertain whether the tubes have a special fibrous coat

or are simple channels in the fibrous structure. They are here lined with pavement-epithelium. In the vasa efferentia and the epididymis, we have a fibrous membrane, with longitudinal and circular fibres of involuntary muscular tissue, and a lining of ciliated epithelium, described by Becker in the bull and the horse,[1] and noted by Kölliker in the human subject.[2] The movement of the cilia is toward the vas deferens. In the lower portion of the epididymis, the cilia are absent. The tubular structures of the testicle, the epididymis, and the commencement of the vas deferens are shown in Fig. 30.

At the lower portion of the epididymis, communicating with the canal, there is usually found a small mass, formed of a convoluted tube of variable length, called the vas aberrans of Haller.[3] (*i.*, Fig. 30.) This is sometimes wanting, and its function, which cannot be very important, is unknown.

Vas Deferens.—The excretory duct of the testicle extends from the epididymis to the prostatic portion of the urethra, and is a continuation of the single tube which forms the body and globus minor of the epididymis. It is somewhat tortuous near its origin, and becomes larger at the base of the bladder, just before it is joined by the duct of the seminal vesicle. Near its point of junction with this duct, it again becomes narrower. Its entire length is nearly two feet.

The course of the vas deferens is in the spermatic cord to the external abdominal ring, through the inguinal canal to the internal ring, where it leaves the blood-vessels, passes beneath the peritoneum to the side of the bladder, then along the base of the bladder by the inner side of the seminal vesicle, finally joining the duct of the seminal vesicle, the com-

[1] BECKER, *Ueber Flimmerepithelium und Flimmerbewegung im Geschlechtsapparate der Säugethiere und des Menschen.—Untersuchungen zur Naturlehre des Menschen und der Thiere*, Frankfurt a. M., 1857, Bd. ii., S. 77.

[2] KÖLLIKER, *Éléments d'histologie humaine*, Paris, 1868, p. 676.

[3] HALLER, *Elementa Physiologiæ*, Bernæ, 1765, tomus vii., p. 449.

mon tube forming the ejaculatory duct, which opens into the prostatic portion of the urethra.

The walls of the vas deferens are thick, abundantly supplied with vessels and nerves, and provided with an external fibrous, a middle muscular, and an internal mucous coat. The greater part of that portion of the tube which is connected with the bladder is dilated and sacculated. The fibrous coat is composed of strong connective tissue. The muscular coat presents three layers; an external, rather thick layer of longitudinal fibres, a thin, middle layer of circular fibres, and a thin, internal layer of longitudinal fibres, all of the non-striated variety. By the action of these fibres, the vessel may be made to undergo energetic peristaltic movements, and this has followed galvanization of that portion of the spinal cord corresponding to the fourth lumbar vertebra, which is described by Budge as the genito-spinal centre.[1]

The mucous membrane of the vas deferens is pale, thrown into longitudinal folds in the greatest part of the canal, and presents numerous additional rugæ in the sacculated portion, these rugæ enclosing little, irregular, polygonal spaces. The membrane is covered with columnar epithelium, which is not ciliated. In the sacculated portion, are numerous mucous glands.

Attached to the vas deferens, near the head of the epididymis, is a little mass of convoluted and sacculated tubes, called the organ of Giraldès,[2] or the corpus innominatum. This body is from $\frac{1}{6}$ to $\frac{1}{3}$ of an inch long and $\frac{1}{12}$ of an inch broad. Its tubes are lined with cells of pavement-epithelium, which are often filled with fatty granules. Generally, the tubes present only blind extremities, but some of them occasionally communicate with the tubes of the epididymis. This organ has no physiological importance. It is regarded

[1] Budge, *Lehrbuch der speciellen Physiologie des Menschen*, Leipzig, 1862, S. 787.

[2] Giraldès, *Recherches anatomiques sur le corps innominé.—Journal de la physiologie*, Paris, 1861, tome iv., p. 1, *et seq.*

by Giraldès as a remnant of the Wolffian body, analogous to the parovarium.

Vesiculæ Seminales.—Attached to the base of the bladder and situated externally to the vasa deferentia, are the two vesiculæ seminales. These bodies are each composed of a coiled and sacculated tube, from four to six inches in length when unravelled, somewhat convoluted, in the natural state, into an ovoid mass which is firmly bound to the vesical wall. The structure of the seminal vesicles is not very unlike that of the sacculated portion of the vasa deferentia. They have an external fibrous coat, a middle coat of muscular fibres, and a mucous lining. Muscular fibres pass over these vesicles from the bladder, both in a longitudinal and in a circular direction, and serve as compressors, by the action of which their contents may be discharged. The mucous coat is pale, finely-reticulated, and is covered with cells of polygonal epithelium, nucleated and containing brownish granules. No mucous glands have been found in its substance.

The vesiculæ seminales undoubtedly serve, in part at least, as receptacles for the seminal fluid, as their contents often present a greater or less number of spermatozoids. The essay of John Hunter on the vesiculæ seminales, first published in 1786, in which the idea was advanced that they did not serve as receptacles for the semen, showed that they produced an independent secretion which became mixed with the product of the testicles in ejaculation; but this opinion was not based upon microscopical observations, and the presence or absence of the spermatozoids was not noted.[1] Although the mucous membrane of the vesicles seems to produce an independent secretion, the presence of glands has not been demonstrated. The fact that the fluid capable of fecundating the ovum is produced only by the testicles, that the

[1] HUNTER, *Observations on the Glands situated between the Rectum and Bladder, called Vesiculæ Seminales.—Observations on certain Parts of the Animal Œconomy*, London, 1792, p. 31, *et seq.*

spermatozoids are the true fecundating elements of the male, and that these are developed in the testicles, shows that the spermatozoids found in the seminal vesicles pass into their cavity from the vasa deferentia.

The ejaculatory ducts are formed by the union of the vasa deferentia with the ducts of the vesiculæ seminales on either side, and open into the prostatic portion of the urethra. Except that their coats are much thinner, they have essentially the same structure as the vasa deferentia.

Prostate.—Surrounding the commencement of the urethra, including what is known as its prostatic portion, is the prostate gland or body. This organ, except as it secretes a fluid which forms a part of the ejaculated semen, has chiefly a surgical interest, so that it is unnecessary to describe minutely its form and relations. It is enveloped in an exceedingly dense, fibrous coat, contains numerous glandular structures opening into the urethra, and presents a great number of non-striated, with a few striated muscular fibres, some just beneath the fibrous coat and others penetrating its substance and surrounding the glands.[1]

The glands of the prostate are most distinct at that portion which lies behind the urethra. In the posterior portion of this canal, are found about twenty openings, which lead to tubes ramifying in the glandular substance. These tubes are formed of a structureless membrane, branching as it penetrates the gland. They present hemispherical diverticula in their course, and terminate in dilated extremities, which are looped and coiled. In the deeper portions of the tubes, the epithelium is columnar or cubical, becoming tesselated near their openings, and sometimes laminated.

The prostatic fluid, according to Robin, is secreted only at the moment of ejaculation.[2] Its characters will be consid-

[1] KLEIN, in STRICKER, *Manual of Human and Comparative Histology*, The New Sydenham Society, London, 1872, vol. ii., p. 297.

[2] ROBIN, *Leçons sur les humeurs*, Paris, 1867, p. 358.

ered under the head of the seminal fluid; but we may here note that it has been thought by Kraus, that the prostatic fluid has the important function of maintaining the vitality of the spermatozoids. "The spermatozoa, in the absence of the prostatic fluid, cannot live in the mucous membrane of the uterus of mammalia; but with its aid they may live for a long time in the uterine mucus, often more than thirty-six hours."[1]

Glands of the Urethra.—Anterior to the prostate, opening into the bulbous portion of the urethra, are two small racemose glands, called the glands of Méry or of Cowper. These have each a single excretory duct, are lined throughout with cylindrical epithelium, and secrete a viscid, mucus-like fluid, which forms a part of the ejaculated semen. Sometimes there exists only a single gland, and occasionally, though rarely, both are absent. Their function is probably not very important.

The glands of Littre, found throughout the entire urethra, and most abundant on its anterior surface, are simple racemose glands, extending beneath the mucous membrane into the muscular structure, presenting here four or five acini. As these acini are thus surrounded by muscular fibres, we can readily understand how their secretion may be pressed out during erection of the penis. They are lined throughout with columnar or conoidal epithelium, and secrete a clear and somewhat viscid mucus, which is mixed with the ejaculated semen.

Male Elements of Generation.

The ejaculated seminal fluid contains the male elements of generation; but it must be remembered that the complex fluid known as the semen is composed of anatomical elements

[1] KRAUS, *Preliminary Communication concerning the Function of the Prostate Gland.*—*Medical Times and Gazette*, London, 1871, vol. i., p. 170. A second and a more elaborate communication in the same volume of the *Medical Times and Gazette* is devoted mainly to the pathology of the prostate.

developed in the testicle itself, mixed with the secretion of the vasa deferentia, of the vesiculæ seminales, of the glands of the prostate, and of the glands of the urethra. As we shall see when we come to discuss the mechanism of fecundation of the ovum, the spermatozoids are the essential male elements, and these are produced in the substance of the testicle, by a process analogous to that of the development of other true anatomical elements, and not by the mechanism with which we are familiar in secreting glands. The testicles cannot be regarded strictly as glandular organs. They are analogous to the ovaries, and are the only organs in which spermatozoids can be developed, as the ovaries are the only organs in which the ovum can be formed. If the testicles be absent, the power of fecundation is lost, none of the fluids secreted by the accessory organs of generation being able to perform the functions of the true fecundating elements.

In the healthy male, at the climax of a normal venereal orgasm, from half a drachm to a drachm of seminal fluid is ejaculated with considerable force from the urethra, by an involuntary muscular spasm. This fluid is slightly mucilaginous, grayish or whitish, streaked with lines more or less opaque, and evidently contains various kinds of mucus. It has a faint and peculiar odor, *sui generis*, which is observed only in the ejaculated fluid and not in any of its constituents examined separately. It is a little heavier than water, and does not mix with it or dissolve. After ejaculation, it becomes jelly-like and dries into a peculiar, hard mass, which may be softened by the application of appropriate liquids. The liquid is not coagulated by heat and does not contain albumen. Its reaction is faintly alkaline. It contains, in the human subject, from 100 to 120 parts of solid matter per 1000.[1]

The chemical constitution of the semen has not been very thoroughly investigated and does not present the same physiological interest as its anatomical characters. Aside from

[1] ROBIN, *Leçons sur les humeurs*, Paris, 1867, p. 366.

the anatomical elements derived from the testicles and the genital passages, it presents an organic principle (spermatine) which has nearly the same chemical characters as ordinary mucosine. It also contains a considerable quantity of phosphates, particularly the phosphate of magnesia. During desiccation, the characteristic crystals of this salt usually make their appearance; and, in the decomposed fluid, we frequently find crystals of the triple phosphates.

The composite character of the seminal fluid will be better understood if we examine briefly the properties of the different mucous secretions which enter into its composition.

In the dilated portion of the vasa deferentia, the mucous glands secrete a fluid which is the first added to the spermatozoids as they come from the testicles. This fluid is brownish or grayish, and contains epithelium, and small, rounded granulations, which are dark and strongly refractive. The liquid itself is very slightly viscid.

In the vesiculæ seminales, there is a more abundant secretion of a grayish fluid, with epithelium, little colorless concretions of nitrogenized matter, called by Robin, sympexions,[1] and a few leucocytes.

The glandular structures of the prostate produce a creamy secretion, containing numerous fine granulations. It is chiefly to the admixture of this fluid that the semen owes its whitish appearance. Finally, as the semen is ejaculated, it receives the exceedingly viscid secretion of the glands of Cowper, a certain amount of stringy mucus from the follicles of the urethra, with, perhaps, a little of the urethral epithelium.

Anatomically considered, the seminal fluid contains no important elements except the spermatozoids, the various secretions we have mentioned serving simply as a vehicle for the introduction of these bodies into the generative passages of the female. We shall therefore consider only the structure of the spermatozoids, their movements, and the process of their development.

[1] Littré et Robin, *Dictionnaire de médecine*, Paris, 1873, Article, *Sympexion*.

Spermatozoids.—In August, 1677, a German student, named Von Hammen,[1] discovered the spermatozoids in the human semen, and exhibited them to Leeuwenhoek, who studied them as closely as was possible with the instruments at his command. For a long time, they were regarded as living animalcules; though now they are considered simply as peculiar anatomical elements, endowed with movements, like ciliated epithelium. These elements are developed within the seminiferous tubes, by a process which has been most elaborately and accurately described by Kölliker. They differ, not so much in their mode of development as in their form, in different animals. We shall describe, however, only the spermatozoids of the human subject, and we find that the history of their development, as given by Kölliker, has not been essentially modified by more recent researches.

If we examine a specimen of the fluid taken from the vesiculæ seminales of an adult who has died suddenly, or the ejaculated semen, we find that it contains, in addition to the various accidental or unimportant anatomical elements which we have mentioned, innumerable bodies, resembling animalcules, which present a flattened, conoidal head and a long, tapering, filamentous tail. The caudate appendage is in active motion, and the spermatozoids move about the field of view with considerable rapidity and force, pushing aside little cor-

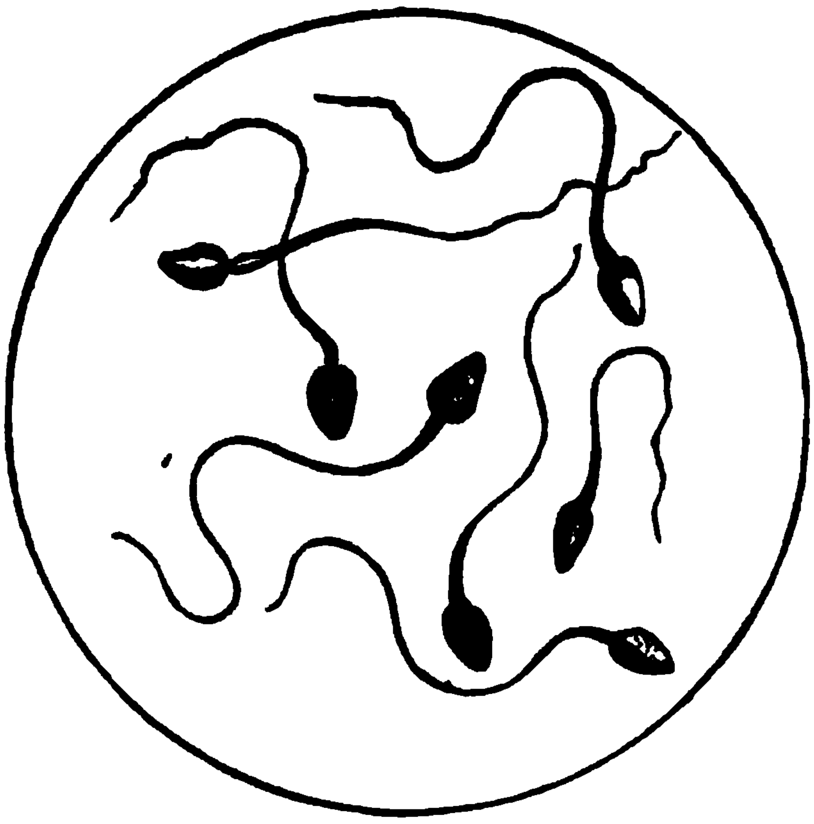
[1] LEEUWENHOEK, *Epistolæ*, Lugd. Batav., 1719, tomus i., p. 59.

The discovery of the spermatozoids marks an era in the history of generation, as it was the first positive fact in opposition to the commonly-received opinion that fecundation was accomplished by the *aura seminalis*, or vapor exhaled from the seminal fluid. It is curious, however, that we are not able to state positively the correct name of the discoverer. Leeuwenhoek, from whose original work the above reference has been taken, calls the name Hammius, which is evidently a German name rendered into Latin. Milne Edwards calls the name Ham. (*Leçons sur la physiologie*, Paris, 1863, tome viii., p. 339.) Longet spells the name Hamm. (*Traité de physiologie*, Paris, 1869, tome iii., p. 781.) Sprengel (*Histoire de la médecine, traduite par* JOURDAN, Paris, 1815, tome iv., p. 309) speaks of the discoverer as a young physician of Dantzick, Louis de Hammen (probably Von Hammen). The name is known in the history of physiology chiefly, if not entirely, from the letters of Leeuwenhoek.

puscles or granules with which they come in contact. This is supposed to be an indication of the vitality of the spermatozoids, which are not thought to be capable of fecundating the ovum after their movements have ceased. Under favorable conditions, particularly in the generative passages of the female, the movements continue for days; and this fact is important, as we shall see hereafter, in its bearing upon the limits of the time of fecundation.

Microscopical examination does not reveal any very distinct structure in the substance of the spermatozoids. The head is about $\frac{1}{5000}$ of an inch long, $\frac{1}{8000}$ of an inch broad, and $\frac{1}{25000}$ of an inch in thickness. The tail is about $\frac{1}{500}$ of an inch in length. La Valette St. George has found, in man and many of the inferior animals, the "intermediate segment" described first by Schweigger-Seidel,[1] though he does not agree with Schweigger-Seidel that this portion is motionless.[2] The length of the intermediate segment is about $\frac{1}{4000}$ of an inch. It is usually described as the beginning of the tail; and the only difference between this and other portions is that it is a little thicker.

FIG. 81.



Human spermatozoids. Magnified 800 diameters. (LUSCHKA, *Anatomie des Menschen*, Tübingen, 1864, Bd. ii., S. 272.)

According to Kölliker, water speedily arrests the movements of the spermatozoids, which may be restored by the ad-

[1] SCHWEIGGER-SEIDEL, *Ueber die Samenkörperchen und ihre Entwicklung.—Archiv für mikroskopische Anatomie*, Bonn, 1865, Bd. i., S. 319.

[2] LA VALETTE ST. GEORGE, in STRICKER, *Manual of Human and Comparative Histology*, The New Sydenham Society, London, 1872, vol. ii., p. 151.

dition of dense saline and other solutions. All of the alkaline animal fluids of moderate viscidity favor the movements, while the action of acid or of very dilute solutions is unfavorable. The movements are suspended by extreme cold, but return when the ordinary temperature is restored.[1]

Before the age of puberty, the seminiferous tubes are much smaller than in the adult, and contain small, transparent cells, which, in their form and arrangement, resemble epithelium. As puberty approaches, however, the tubes become larger, and the cell-contents increase in size. At this time, there seem to be two kinds of cells; an epithelium, in the form of irregularly-shaped cells, lining the tubes, and rounded cells, containing one or more nuclei, some of the cells appearing to be in process of segmentation. Many of the cells lining the tube, according to La Valette St. George, present a rounded portion, with a large, clear nucleus, applied to the tube-wall, each with a caudate prolongation projecting into the tube.[2] Sometimes the projections from the different cells anastomose with each other, forming a kind of network, which is possibly the appearance of segmentation, described by Kölliker.

In the central portions of the tubes of the adult, are rounded vesicles, from $\frac{1}{2250}$ to $\frac{1}{370}$ of an inch in diameter, each containing from two to twenty transparent nuclei measuring from $\frac{1}{5000}$ to $\frac{1}{3000}$ of an inch. In these, which are called the seminal cells, La Valette St. George has discovered amœboid movements.[3] The large vesicles with multiple nuclei are the seat of development of the spermatozoids. The nuclei of the vesicles appear to be transformed into the heads of the spermatozoids, and the filamentous appendages, which are seen in the vesicles in various stages of formation, are developed gradually. It often occurs that,

[1] Kölliker, *Éléments d'histologie humaine*, Paris, 1868, p. 683.

[2] La Valette St. George, in Stricker, *Manual of Human and Comparative Histology*, The New Sydenham Society, London, 1872, vol. ii., p. 138.

[3] *Op. cit.*, p. 141.

when from ten to twenty spermatozoids are developed in a single vesicle, the heads and tails are arranged regularly, side by side; but when but two or three are observed, their arrangement is irregular. The vesicular envelopes finally disappear and the spermatozoids are liberated; but this only occurs in the rete testis and in the epididymis. In the epididymis and the vasa deferentia, the spermatozoids are

FIG. 82.

Development of the spermatozoids in the rabbit.—*a*, *a*, spermatozoids; *b*, spermatic cell containing fourteen nuclei, two of which contain each a head of a spermatozoid developed; *c*, spermatic cell containing two secondary cells, each one provided with a nucleus from which two spermatozoids are to be developed; *d*, spermatic cell with one nucleus; *e*, spermatic cell containing a secondary cell with a nucleus; *h*, bundle of spermatozoids. (Longet, *Traité de physiologie*, Paris, 1869, p. 900.)

motionless, though they are not enclosed in vesicles, apparently from the density of the substance in which they are embedded; for movements are sometimes presented when the contents of the vasa deferentia are examined with the addition of water or saline solutions. Once in the vesiculæ

seminales, or after ejaculation, the spermatozoids are invariably in active motion.[1]

The semen thus developed and mixed with the various secretions before mentioned is found during adult life and even at an advanced age; and, under physiological conditions, it contains innumerable spermatozoids in active movement. But if sexual intercourse be frequently repeated at short intervals, the ejaculated fluid becomes more and more transparent, homogeneous, and scanty, and may consist of a small amount of secretion from the vesiculæ seminales and the glands opening into the urethra, without spermatozoids, and consequently deprived of fecundating properties.

In old men, the seminal vesicles may not contain spermatozoids; but this is not always the case, even in very advanced life. Instances are constantly occurring of men who have children in their old age, in which the paternity of the offspring can hardly be doubted. Duplay, in 1852, examined the semen of a number of old men, and found, in about half the number, spermatozoids, normal in appearance and quantity, though, in some, the vesiculæ seminales contained either none or very few. Some of the individuals in whom the spermatozoids were normal were between seventy-three and eighty-two years of age.[2] More recently, M. A. Dieu has investigated the same question. In his conclusions, adding to his own observations the fifty-one cases noted by Duplay, he gives the following results, in one hundred and fifty-six old men:

[1] Kölliker, *Éléments d'histologie humaine*, Paris, 1868, p. 678, *et seq.*

[2] Duplay, *Recherches sur le sperme des vieillards.—Archives générales de médecine*, Paris, 1852, 4e série, tome xxx., p. 397.

Duplay seems to have been the first, except Wagner, to have demonstrated microscopically the presence of spermatozoids in the vesiculæ seminales of old men, but others had found a liquid like the semen in the vesicles and testicles. Duplay cites a case of this kind reported by Timmius, in an old man of ninety-four. Wagner (*Elements of Physiology*, London, 1841, p. 7) makes the following statement: "I have constantly found seminal animalcules in the fluid of the testis of very aged men; it is only among weakly and decrepid individuals that the procreative faculty is really lost."

"25 sexagenarians gave a proportion, still presenting spermatozoids, of 68·5 per 100.

"76 septuagenarians gave a proportion, still presenting spermatozoids, of 59·5 per 100.

"51 octogenarians gave a proportion, still presenting spermatozoids, of 48 per 100.

"4, having passed the age of 90 years, gave entirely negative results."

The oldest man, in the cases reported by Duplay, was eighty-two, and, in those noted by Dieu, eighty-six years, which latter Dieu fixes as the limit, not having observed spermatozoids after that age. The observations were made by examining the contents of the generative passages twenty-four hours after death. Some of the subjects died of acute, and others, of chronic diseases; but the mode of death did not present any differences in the cases classed with reference to the presence of spermatozoids. As a result of his own and other investigations, Dieu comes to the conclusion that the power of fecundation in the male often persists for a considerable time after the power of copulation has been lost simply from incapacity for erection of the penis.[1]

[1] Dieu, *Recherches sur le sperme des vieillards.—Journal de l'anatomie et de la physiologie*, Paris, 1867, tome iv., p. 449, *et seq.*

CHAPTER XIV.

FECUNDATION.

Coitus—Action of the male—Erection—Ejaculation of semen—Action of the female—Erection of the female organs—Action of the cervix and os uteri during sexual excitement—Entrance of spermatozoids into the uterus—Course of the spermatozoids through the female generative passages—Duration of vitality of spermatozoids and ova—Mechanism of fecundation—Determination of the sex of offspring—Hereditary transmission—Superfecundation—Influence of the maternal mind on offspring—Union of the male with the female element of generation—Passage of the spermatozoids through the vitelline membrane.

As far as the male is concerned, coitus is rendered possible by erection of the penis. This may occur before puberty, but, at this time, intercourse cannot be fruitful. As we have seen in a previous chapter, coitus may be impossible in old age, from absence of the power of erection; but spermatozoids may still exist in the vesiculæ seminales, and fecundation might occur, if the seminal fluid could be discharged into the generative passages of the female. Coitus may take place in the female before the age of puberty or after the final cessation of the menses, but intercourse cannot then be fruitful. There are sufficiently numerous examples of conception following what would be called imperfect intercourse, as in cases of unruptured hymen, deformities of the male organs, etc., to show that actual penetration of the male organ is not essential, and that fecundation may occur, provided the seminal fluid find its way into even the lower part of the vagina. Conception has also followed intercourse, when the female has been insensible or entirely passive; but we shall only consider the physiology of com-

plete and normal intercourse, when both the male and female participate, more or less, in the sexual act.

Action of the Male.—The act of sexual intercourse is preceded, in the male, by a longer or shorter period of excitement, the most important manifestation of which is erection and rigidity of the penis. This is largely controlled by the nervous system. It may be due to distention of the vesiculæ seminales, and, perhaps, of the tubes of the testicle and epididymis after prolonged continence, to the imagination, or to the presence or thought of a female exciting desire. The excitement may, also, be arrested by a sudden feeling of disgust, modesty, or fear; and it sometimes happens that the excitement is so intense that the male organ becomes flaccid without ejaculation. An occurrence of this kind frequently occasions such an amount of mortification and apprehension for the future, that, from the mere dread of a similar accident, there is frequently an incapacity for intercourse when, in all other respects, the conditions are absolutely normal. Physicians have frequent occasion to observe this, especially in the newly-married, who are often afflicted with the fear of permanent sexual incapacity, and seek professional advice. This illustrates the influence of the nervous system upon the sexual organs, in the absence of diseased conditions.

Unlike certain of the lower animals, the human subject presents no distinct periodicity in the development of the spermatozoids; but, in reiterated connection, an excitement and orgasm may occur when the ejaculated fluid has no fecundating properties. Such frequently-repeated sexual acts are abnormal; but, from a purely physiological point of view, prolonged continence is equally unnatural and may react unfavorably on the nervous system. No absolute or even approximative rule can be laid down with regard to the frequency with which intercourse may take place within physiological limits. We may assume that these conditions are fulfilled, first, when intercourse is confined within the

limits of legitimacy, after the unusual excitement of novelty has passed; second, when both the male and female are in perfect health, and no undue degree of lassitude follows coitus, after a proper period of repose; third, when there is no marked diminution of sexual desire, except that which may be accounted for by age; fourth, when pregnancy occurs at proper intervals, progresses normally, and is followed by the normal period of lactation; fifth, when menstruation is regular, and when there is a period, usually after the cessation of the flow, during which there is unusual sexual excitement, responded to by the male, and disappearing after the sexual desires have been satisfied. It may be somewhat rare to find these conditions fulfilled in all respects, as so few men and women in civilized life are absolutely normal during adult age, and as the sources of unnatural sexual excitement are so numerous; but they approximatively represent the physiological performance of the generative functions in both sexes. It is true that the female can frequently endure sexual excesses better than the male, because she is more passive and may often not participate in the venereal excitement; but if we assume that intercourse is physiologically confined within the limits fixed by social laws, the same rules as regards frequency of the sexual act should apply to both. It is certain that intercourse is not normal in the female during menstruation or during the greater part of utero-gestation; and, at these times, it is physiological that the male should be continent. Taking our view chiefly from what appear to be the sexual requirements of the female, intercourse most properly takes place at the time following the menstrual flow when there is usually a certain amount of sexual excitement, and this should not be immediately repeated, though it may be physiological after a few days. As sexual excitement is gratified and diminishes, intercourse, as far as the desires of the female are concerned, is suspended, and it does not take place to any great extent during pregnancy. This seems to correspond with the normal progress of the genera-

tive functions, as we have traced it in the female. It is evident that this is a subject of great delicacy, and one that is with difficulty brought to the requirements of rigid scientific inquiry; still it can hardly be avoided in a full account of the physiology of generation, and is a question often presented to the practical physician.

Although we have not yet considered fully the mechanism of erection, but little remains to be said on this subject after our discussion, in another volume, of the general structure of erectile tissues.[1] The cavernous and spongy bodies of the penis are usually taken as the type of erectile organs. In these parts, the arteries are large, contorted, provided with unusually thick muscular coats, and connected with the veins by vessels considerably larger than the true capillaries. They are supported by a strong fibrous net-work of trabeculæ which contains non-striated muscular fibres; so that, when the blood-vessels are completely filled, the organ becomes enlarged and hardened, and can penetrate the vagina. The researches of Eckhard on the nerves of erection show conclusively that the vessels of erectile tissues are distended by an enlargement of the arterioles of supply, and that there is not simply a stasis of blood produced by constriction of the veins, except, perhaps, for a short time, during the period of most intense venereal excitement. In experiments upon dogs, Eckhard discovered a nerve derived from the sacral plexus, stimulation of which produced an increase in the flow of blood through the penis, attended with all the phenomena of erection. This nerve arises by two roots at the sacral plexus, from the first to the third sacral nerves. In the experiments referred to, by a comparison of the quantity of venous blood coming from the penis before and during the stimulation of the nerve, Eckhard found a great increase during erection.[2] It is probable that, in addition to the arterial

[1] See vol. i., Circulation, p. 337.

[2] ECKHARD, *Experimentalphysiologie des Nervensystems*, Giessen, 1866, S. 287. Robin (*Observations sur la constitution du tissue érectile, lues à la Société de*

dilatation, when the penis attains its maximum of rigidity, there is a certain amount of obstruction to the outflow of blood, by compression of the veins, and that the rigidity is increased by contraction of the trabecular muscular fibres of the corpora cavernosa.

During erection, the penis becomes exquisitely sensitive, especially at the glans; introduction of the organ into the vagina, pressure by the constrictor muscle, and friction increase this sensibility, until the venereal orgasm occurs. At this time, there is a peculiar and indefinable sensation, almost immediately followed by spasmodic contractions of the vesiculæ seminales and the ejaculatory muscles, and, at the climax of the orgasm, the semen is discharged from the urethra with considerable force. This is followed by a feeling of lassitude, a general sense of fatigue of the generative organs, flaccidity of the penis, and it is some time before the venereal appetite can be again excited. Although this is the physiological mechanism of a seminal discharge, friction of the parts is not absolutely necessary, as is shown by the occurrence of orgasm during sleep, which is liable to take place in healthy men after prolonged continence.

After the seminal fluid has been ejaculated during intercourse, the generative act, as far as the male is concerned, is accomplished. It now remains for us to study the action of the female, and the process by which the spermatozoids are brought in contact with the ovum.

Action of the Female.—If we can credit the statements made to physicians in their professional intercourse—and we have no other reliable source of information—there are some females, in whom the generative function is performed, even to the extent of bearing children, who have no actual knowledge of a true venereal orgasm; but there are others

Biologie, dans sa séance du 27 *août*, 1864, p. 16) was the first to distinctly ascribe erection to dilatation of the arteries of supply, under the influence of the nervous system, without obstruction of the veins.

who experience an orgasm fully as intense as that which accompanies ejaculation in the male. There is, therefore, the important difference in the sexes, that preliminary excitement and an orgasm are necessary to the performance of the generative act in the male, but are not essential in the female. Still, there can be scarcely a doubt but that venereal excitement in the female facilitates conception, other conditions being favorable.

The first intercourse in the female is usually more or less painful, on account of rupture of the hymen, and the external organs are unduly sensitive until the parts are healed. After this, if there be a preliminary excitement, there is a certain amount of erection of the clitoris, which corresponds to the penis, and of the erectile bulbs situated at the vaginal orifice. There is also an increase in the secretions about these parts, and even an ejaculation from two glands opening near the labia minora, called the glands of Bartholinus, which correspond to the glands of Cowper in the male. How far the internal erectile parts participate at this time, it is difficult to determine. By the friction against the clitoris, which, at its maximum of erection, is directed toward the axis of the vagina, against the vaginal walls, and probably, also, by the contact of the glans penis with the neck of the uterus, the excitement of the female increases, the vessels of the vagina become turgid, the secretion of mucus by the external organs becomes abundant, and this finally culminates in an orgasm, similar to that experienced by the male, with a farther increase in the secretion of the glands at the vaginal orifice. As we have stated in our history of the discharge of the ovum from the Graafian follicle, this congestion and excitement may hasten the rupture of a ripe follicle in the human female, as it undoubtedly does in many of the lower animals; but follicles certainly rupture independently of coitus. There is a certain degree of lassitude in the female following sexual intercourse, but this is usually not so marked or so prolonged as in the male.

The most important physiological point in this connection is with regard to the probable action of the internal organs of the female during sexual excitement. We have already studied what has been described by Rouget as the erectile tissue of the uterus and ovaries. Whether this be or be not a true erectile tissue, seems to be rather a question of definition. The blood-vessels certainly have an erectile arrangement; still, they are not enclosed by those distinct, fibrous trabeculæ which are observed in the penis. In the body of the uterus and in the ovaries, the idea of erection during sexual excitement rests simply upon anatomical descriptions and artificial distention of the vessels after death, and the parts cannot be investigated during life; but it is different with the neck of the uterus, as we shall see farther on; and, upon this point, we may refer to a very remarkable paper, by Dr. Joseph R. Beck, of Fort Wayne, Indiana, which has hardly received, in this country, the attention it deserves.[1] Dr. Beck's observations relate to the question, "How do the spermatozoa enter the uterus?" and, when we consider that it has been positively demonstrated that spermatozoids find their way to the surface of the ovaries, we can appreciate the importance of any reliable observations with regard to the action of the internal organs during coitus.

August 11, 1872, Dr. Beck was called to see a lady, thirty-two years of age, of nervous temperament, blonde, married eight years, with one child, a son, living and seven years old. She had an abortion six years before, and has suffered from symptoms indicating uterine disease ever since. She commenced to menstruate at fourteen. Examination with the finger showed that the os uteri was just inside the vulva, and McIntosh's stem-pessary was introduced. The rest of the history, as the observation is so remarkable, we quote in full:

"Calling at the residence of the patient next day, for the

[1] BECK, *How do the Spermatozoa enter the Uterus?—Saint Louis Medical and Surgical Journal*, 1872, New Series, vol. ix., p. 449, *et seq.*

purpose of adjusting the uterine supporter, I made an examination by the touch, and upon introducing my finger between the pubic arch and the anterior lip of the prolapsed cervix, I was requested by her to be very careful in manipulating those parts, as she was very prone, by reason of her passionate nature, to have the sexual orgasm produced by a very slight contact of the finger. Indeed she stated that this had more than once occurred to her, when making digital investigation of herself. Here then was an opportunity never before offered any one to my knowledge, and one not to be lost on any consideration. Carefully separating the vulvæ with my left hand, so that the os uteri was brought clearly into view in a strong light, I swept the right forefinger across the cervix twice or three times, when almost immediately the orgasm occurred, and the following is what was presented to my view:

"The os and cervix uteri had been firm, hard, and generally in a normal condition, with the os closed so as not to admit the uterine probe without difficulty; but immediately the os opened to the extent of fully an inch, made five or six successive gasps, drawing the external os into the cervix each time powerfully, and at the same time becoming quite soft to the touch. All these phenomena occurred within the space of twelve seconds time certainly, and in an instant all was as before; the os had closed, the cervix hardened, and the relation of the parts had become as before the orgasm.

"Now I carefully questioned my patient as to the nature of the sensations experienced by her at the period of excitement, and she was positive that they were the same in *quality* as they ever were during coition, even before the occurrence of the prolapse; but admits that they were not exactly the same in *quantity*, believing that during coition the orgasm had *lasted longer*, although not at all or in any respect different as to sensation. I had almost forgotten to make mention of the intense congestion of the parts during the 'crisis,' and introduce the statement here."

Certainly, the description we have just quoted is sufficiently graphic, and the mechanism of the penetration of spermatozoids into the uterus, if this be the action of the cervix during an orgasm, seems simple enough; but it cannot explain fecundation, when it occurs, as it undoubtedly may, without orgasm. In physiological literature, we find numerous allusions to a suction force exerted by the uterus during coitus, but this is most frequently stated as of possible or probable occurrence, without being sustained by any positive observations.[1] Still, as early as 1846, we find a direct observation, recorded by Litzmann, as follows:

After quoting remarks of a similar nature, made by Bond, Vallisneri, Dionis, Haller, and Günther, Litzmann states: "I myself lately had the opportunity, in an internal exploration of a young and very erethistic female, of observing that suddenly the uterus assumed a more perpendicular position, was drawn more deeply into the pelvis, the lips of the os uteri immediately became separated, the os became rounded, softer and accessible to the finger, and immediately the highest sexual excitement was betrayed by the respiration and voice."[2]

In considering the mechanism of the penetration of spermatozoids into the uterus, it is also necessary to take into account the secretions, particularly of the mucous glands at the

[1] Pouchet (*Théorie positive de l'ovulation spontanée et de la fécondation*, Paris, 1847, p. 387), in treating of the question of penetration of spermatozoids in connection with a "convulsive spasm" of the internal organs during intercourse, makes the following statement:

"According to my view, the spasm in question, by energetically contracting the uterus and the tubes during intercourse, tends to diminish the capacity and abolish the cavity of these organs, so that, during this action, the contained mucus is totally expelled. But, when the spasm ceases, the uterus and the tubes dilating give again to their cavity the ordinary capacity, and then, by simple hydrostatic laws, the seminal fluid discharged into the vagina is in part drawn into the uterus; it then enters its cavity in greater or less abundance, and finally extends into the canals which lead from it."

[2] Litzmann, *Schwangerschaft*, in Wagner, *Handwörterbuch der Physiologie*, Braunschweig, 1846, Bd. iii., Erste Abtheilung, S. 53.

neck. Després mentions a fluid secreted by glands in the cervix uteri, which is ejaculated during the orgasm and facilitates the entrance of spermatozoids.[1] Most writers of the present day admit that, during the height of the orgasm, there is an ejaculation from the uterus of a small amount of alkaline mucus.[2] That an erection of the cervix, followed by sudden relaxation and opening of the os, may occur, cannot be doubted, and there is no evidence of a muscular action in the uterus sufficient to project this fluid forcibly, as the semen is discharged by the male. Assuming that the views just stated be correct, we can readily understand how the neck may be erected and hardened during the orgasm, extruding an alkaline mucus, that the semen is ejaculated forcibly toward the uterus and becomes mixed with the mucus, and that the sudden relaxation of the cervix and opening of the os may exert a force of aspiration, and thus draw in the fecundating elements. Certain it is that spermatozoids may be found in the mucus of the cervix a very short time after coitus. It is possible, also, that the sexual connection may be occasionally even more intimate, and that a portion of the glans penis may be actually embraced by the dilated cervix, though this must be unusual. This latter idea of the establishment of a "continuous canal" during intercourse is one that was advanced by many of the older writers.

Rather a strong argument in favor of the view that the spermatozoids are imprisoned, as it were, in the cervical mucus soon after ejaculation, is the fact that vaginal injections immediately after intercourse, which are frequently resorted to to prevent conception, often fail to produce the desired result, even when they are so thorough as to wash out the vagina completely.

While we must accept as probable the view that the ute-

[1] Després, *Traité iconographique de l'ulcération et des ulcères du col de l'utérus*, Paris, 1870, p. 19, *et seq.*

[2] Wernich, *Ueber die Erectionsfähigkeit des unteren Uterusabschnittes und ihre Bedeutung.—Beiträge zur Geburtshülfe und Gynäkologie*, Berlin, 1872, Bd. i., S. 301.

rus may draw into the neck an alkaline mucus previously ejaculated, and with it a certain amount of seminal fluid, the fact that conception may take place without orgasm on the part of the female, and even without complete penetration of the male organ, shows that the action we have described is not absolutely essential, and that the semen may find its way into the uterus in some other way, which it is certainly very difficult to explain.

Course of the Spermatozoids through the Female Generative Passages.

The spermatozoids, once within the cervix uteri, and in contact with the alkaline mucus, which increases the activity of their movements, may pass through the uterus, into the Fallopian tubes, and even to the surface of the ovaries. Precisely how their passage is effected, it is impossible to say. We can only attribute it to the movements of the spermatozoids themselves, to capillary action, and to a possible peristaltic action of the muscular structures, and must acknowledge that these points have as yet been incapable of positive demonstration.

In a very interesting memoir by Lott, which contains numerous observations bearing on the mechanism of conception, the experiments upon the behavior of the spermatozoids under the microscope, in the presence of currents observed in the liquid between the two plates of glass, develop some very curious points. It was shown, in these experiments, that motionless spermatozoids followed the currents freely; that when the current in any part of the field was strong, the moving spermatozoids were carried along with it; but that when the current was comparatively feeble, spermatozoids endowed with active movements made their way, as it were, against it.[1] In reflecting upon these observations, it has seemed to us that they offered an explanation, to a certain extent, of the

[1] LOTT, *Zur Anatomie und Physiologie des Cervix Uteri*, Erlangen, 1872, S. 139.

passage of spermatozoids in the Fallopian tubes toward the ovaries. It is undoubtedly true that the ciliary motion in the Fallopian tubes, in which the direction is from the ovaries toward the uterus, would produce a feeble current. This current would naturally direct the heads of the spermatozoids toward the interior, provided it were not too powerful, and the movements of progression would therefore be from without inward. A little reflection makes it evident that, with a feeble current in the Fallopian tubes from within outward, the spermatozoids, if the current were not strong enough to carry them with it, could only progress in the opposite direction; but this cannot explain the passage of the spermatozoids through the uterus itself, where, according to the best authorities, the ciliary current is from without inward.

As regards the human female, we cannot give a definite idea of the time required for the passage of the spermatozoids to the ovaries or for the descent of the ovum into the uterus; and it is readily understood how these questions are almost incapable of experimental investigation. We know, however, that spermatozoids reach the ovaries, and they have been seen in motion on their surface seven or eight days after connection.[1]

There are many elements of uncertainty in all investigations as to the usual or the normal situation of fecundation. As the spermatozoids are found in movement in all parts of the generative passages, the question resolves itself into that of the duration of vitality of the ovum after its discharge; and here we must rely exclusively upon observations made on the inferior animals. Coste, who demonstrated beyond a doubt that fecundation occurs in fowls at or very near the ovary, recognized fully the difficulties attending similar experiments on mammals. He succeeded, however, in two observations on rabbits, in which copulation took place after the period of heat and some time after the discharge of ova.

[1] KÖLLIKER, *Éléments d'histologie humaine*, Paris, 1868, p. 682.

In both of these, he found ova at the superior extremity of the cornua of the uterus, a position which he had found that the ova reached toward the end of the third day. These ova, which were apparently advanced in decomposition, presented no evidence of fecundation, and were enveloped in a dense zone of albumen which they had received from the Fallopian tubes. They were surrounded by spermatozoids in active movement, but none had penetrated the adventitious albuminous covering. From these observations, the conclusion is deduced that fecundation can only take place at the ovary or in the most dilated portion of the Fallopian tubes.[1] When we come to apply these observations to the human subject, we have, in confirmation of them, only the abnormal phenomenon of abdominal pregnancy, which cannot occur unless the ovum have been fecundated at the ovary, afterward falling into the abdominal cavity instead of passing to the uterus. Still, the fact that conception may follow a single intercourse occurring at any time with reference to the menstrual period throws a doubt upon the theory that fecundation takes place only at or near the ovary; and another element of uncertainty is in the fact that we do not know positively that ovulation takes place at any definite time before, during, or after the menstrual period, nor do we know precisely how long the spermatozoids may retain their vitality in the female generative passages.

The question of the duration of vitality of the spermatozoids after their passage into the uterus has an important bearing upon the time when conception is most liable to follow sexual intercourse. The alkaline mucus of the internal organs actually favors their movements; the movements are not arrested by contact with menstrual blood; and, indeed, when the spermatozoids are mixed with the uterine mucus, they simply change their medium, and there is no reason to believe that they may not retain their vitality as well as in the mucus of the vesiculæ seminales. We cannot, there-

[1] Coste, *Développement des corps organisés*, Paris, 1859, tome ii., p. 79, *et seq.*

fore, fix any limit to the vitality of these anatomical elements under physiological conditions; and we cannot say positively that spermatozoids may not remain in the Fallopian tubes and around the ovary, when intercourse has taken place immediately after a menstrual period, until the ovulation following. There is an idea, based upon rather general and indefinite observation, that conception is most liable to follow an intercourse which occurs soon after a monthly period; but it is certain that it may occur at any time. It is extremely probable that, during the unusual sexual excitement which the female generally experiences after a period, the action of the internal organs attending and following coitus presents the most favorable conditions for the penetration of the fecundating elements, and this may explain the more frequent occurrence of conception as a consequence of intercourse at this time.

Mechanism of Fecundation.—In considering the intimate mechanism of fecundation, we may begin with the proposition that this is accomplished by an actual union of the substance of the ovum with a greater or less number of spermatozoids. This fact, which has long since been positively demonstrated by experiments, affords a material explanation of hereditary transmission, not only of maternal, but of paternal physical and mental qualities.

There are many questions connected with hereditary transmission, which, if they were susceptible of any thing approaching a positive scientific explanation, would be of great interest and might appropriately be discussed in a work on physiology; but, although the facts of hereditary influence, as regards the inheritance both of physiological and morbid attributes and tendencies, the influence of the maternal mind on the development of the fœtus, the effects of previous pregnancies, etc., cannot be doubted, their consideration would involve little more than a mere enumeration of remarkable phenomena.

The first question which naturally arises, and which has engaged the attention of ancient as well as modern authors, relates to the conditions which determine the sex of the offspring. The older writers, whose exact physiological knowledge was comparatively limited, were able to present explanations of some of the phenomena of generation, which were more or less satisfactory in their day; but many of these have been contradicted by more recent facts, which have only rendered the causes of the phenomena more obscure. Iconoclasm in physiology is almost a necessary consequence of the acquisition of definite knowledge; and too often the exact student must fail to substitute any thing to supply the places of the broken images of antiquity. This is illustrated in the question of the determination of the sex of offspring. Statistics show clearly enough the proportions between male and female births; but nothing has ever been done in the way of procreating male or female children at will. According to Longet, the proportion of male to female births is about 104 to 105,[1] these figures presenting certain modifications under varying conditions of climate, season, nutrition, etc.; Girou de Buzareingues has shown, by very extensive observations upon certain of the inferior animals, that the preponderance of sex in births bears a certain degree of relation to the vigor and age of the parents; and that old and feeble females fecundated by young and vigorous males bring forth a greater number of males, and *vice versa*;[2] but no exact laws of this kind have been found applicable to the human subject. The idea that one testicle produces males and the other, females, or that the two ovaries have distinct functions in this regard, has no foundation in fact; for men with one testicle, or females with a single ovary, produce offspring of both sexes.[3]

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 821.

[2] GIROU DE BUZAREINGUES, *Reproduction des animaux domestiques.—Journal de physiologie*, Paris, 1827, tome vii., pp. 127, 132; Idem., 1828, tome viii., p. 10; *De la génération*, Paris, 1828, p. 133, *et seq.*

[3] A very interesting case bearing upon the question under consideration has

Two ideas with regard to the determination of sex in the fœtus have obtained at different times. One of these is that the sex is dependent upon nutritive or other conditions subsequent to fecundation, and the other, that the sex is determined at the time of union of the male with the female element. Of these two opinions, the weight of evidence appears to be in favor of the latter. Aside from facts in comparative physiology, it is pretty certain that several spermatozoids are necessary for the fecundation of a single ovum. It may be that, when just enough of the male element unites with the ovum to secure fecundation, or when it might be said that the female element predominates, the fœtus is a female, and when a greater number of spermatozoids unite with the vitellus, the male sex is determined. Such an idea, however, is purely theoretical; and the question of the determination of sex presents thus far hardly the shadow of a satisfactory explanation.

No definite rule can be laid down with regard to the transmission of mental or physical peculiarities to offspring. Sometimes the progeny assumes more the character of the male than of the female parent, and sometimes the reverse is the case, without any reference to the sex of the child; sometimes there appears to be no such relation; and occasionally we note peculiarities derived apparently from grandparents. This is true with regard to pathological as well as physiological peculiarities, as in inherited tendencies to certain diseases, malformations, etc.

A peculiar, and, it seems to be, an inexplicable fact is that previous pregnancies have an influence upon offspring. This is well known to breeders of animals. If a pure-blooded mare or bitch have been once covered by an inferior male,

lately been reported by Prof. Marzolo, of Padua. In a patient, thirty-four years of age, the left ovary was removed for cystic tumor. The woman recovered from the operation, and became pregnant about a year after. She was delivered at full term of twins, a male and a female, and both of the children did well. (*Gazette médicale de Paris*, 1873, No. 44, p. 582.)

in subsequent fecundations, the young are apt to partake of the character of the first male, even if they be afterward bred with males of unimpeachable pedigree. What the mechanism of the influence of the first conception is, we can form no definite idea; but the fact is incontestable. The same influence is observed in the human subject. A woman may have, by a second husband, children who resemble a former husband, and this is particularly well marked in certain instances by the color of the hair and eyes. A white woman who has had children by a negro may subsequently bear children to a white man, these children presenting some of the unmistakable peculiarities of the negro race.

Superfecundation[1] of course does not come in the category of influences such as we have just mentioned. It is not infrequent to observe twins, when two males have had access to the female, which are entirely distinct from each other in their physical character; a fact which is readily explained by the assumption that two ova have been separately fecundated. This view is entirely sustained by observation and experiment. Cases illustrating this point are numerous, but we cite the two following, simply to add to the number of positive observations.

In May, 1869, we received the following written commu-

[1] Superfecundation, by which we mean the fecundation of a second ovum after one has already been fecundated, certainly may take place, as has been shown by cases of twins presenting entirely different physical characteristics. The possibility of superfœtation, by which we understand fecundation of a second ovum after the first has undergone considerable development, has been doubted by many authors. In 1855, Prof. Barker reported a very interesting case of double vagina with double uterus; and this woman, having given birth to a well-developed child, a boy, nine months and one day after her marriage, seventy-four days after the birth of this child, was delivered of a girl. One month after the birth of the second child, she was nursing both children, who were doing well. (FORDYCE BARKER, *Case of Superfœtation.—American Medical Monthly*, New York, 1855, vol. iv., p. 364.) Dr. A. E. M. Purdy, of New York, has had for some time under observation the case of a young girl with a double vagina and a double os uteri. A full report of this case will shortly be published.

nication from Dr. Amos Sawyer, of Hillsboro, Illinois, who seems to have been a close observer of physiological points in the breeding of animals:

"Mr. Adam Vettle, residing two and a half miles southwest of Nocomis, Montgomery County, Illinois, during the spring of 1868, bred a mare to his stallion. A few nights thereafter (he thinks a week) his jack 'broke loose' and staid with the mare until morning—she still being in heat. A few days ago, she gave birth to twins, one a horse, the other a mule colt, both alive and doing well."

The following very interesting communication was received in January, 1869, from Dr. John H. Janeway, Assistant Surgeon U. S. A., and illustrates superfecundation in the human subject; or, at least, that was the view taken by the negro father:

"Frances Hunt, a freedwoman, aged thirty-five years, gave birth to twins, February 4, 1867, in New Kent County, Virginia. One of these twins was black, the other was white. Frances is a mulatto. The black child is much darker than she is. Previous to the parturition, she had given birth to seven children, all single births. She was living at the time of her impregnation in the family of a white man as house-servant, sleeping with a black man at night. She insists, however, that she never had carnal intercourse with a white man. She probably does this because the black man turned her out of his house when he saw that one of the children was white."

This history was accompanied by an excellent photograph of the mother and the two children, a copy of which is given in Fig. 33. One of the children has the color and all the characteristics of the negro, and the other looks like a white child. "The mother and children were inmates of Howard Grove Hospital near this city (Richmond), where the picture was taken, and I saw them frequently. Both children are now dead. The black one died first, teething, the other was killed by a tobacco-plaster applied to its abdomen, it is supposed by its mother.

"The only negro feature in the white child was its nose. There, its resemblance to its mother was perfect. Its hair was long, light, and silky. Complexion brilliant."[1]

FIG. 88.

Mulatto mother with twins, one white and the other black.—From a photograph.

We have already referred to the curious fact that, when a cow gives birth to twins, one male and the other female, the

[1] The very interesting case just cited is not unique in this country. Dunglison, in addition to the well-known case quoted by Buffon, which is often referred to by European writers, gives several instances of twins of different races, and says that this is not uncommon where negro slavery exists. (DUNGLISON, *Human Physiology*, Philadelphia, 1856, vol. ii., p. 485.)

female, which is called a free-martin, is sterile, and presents an imperfect development of the internal organs of generation.[1] This has led to the idea that possibly the same law may apply to the human subject, in cases of twins, one male and the other female; but numerous observations are recorded in gynæcological works, showing the incorrectness of this view, to which we may add the following: The author of the report on Rinderpest to the New York State Agricultural Society, 1867, stated that his father was one of twins, male and female, and that his father's twin sister had borne several children.

It has long been a question whether impressions made on the nervous system of the mother can exert an influence upon the fœtus *in utero*. While many authors admit that violent emotions experienced by the mother may affect the nutrition and the general development of the fœtus, some writers of high authority deny that the imagination can have any influence in producing deformities.[2] It must be admitted that many of the remarkable cases recorded in works on physiology as instances of deformity due to the influence of the maternal mind are not reliable. It is often the case that, when a child is born with a deformity, the mother imagines she can explain it by some impression received during pregnancy, which she only recalls after she knows that the child is deformed. Still, there are cases which cannot be doubted, but which, in the present state of our knowledge of development and the connection between the mother and the fœtus, we cannot attempt to explain. Prof. Dalton, whose accuracy upon such a point cannot be questioned, noted the following: While he was lecturing upon the subject of generation at the College of Physicians and Surgeons of New York, the janitor of the college called his attention to his child, which presented a deformity of the external ear, as

[1] See page 303.

[2] Isidore Geoffrey Saint-Hilaire, *Anomalies de l'organization chez l'homme et les animaux*, Bruxelles, 1837, tome iii., p. 391.

though a portion had been taken off with a sharp instrument. The janitor stated that his wife, during her pregnancy, dreamed that she saw a man with a similar deformity. This dream was very vivid, and she immediately related it to her husband. They both believed that this was the cause of the deformity of the child.[1] It will be remarked, however, that this case rests on the evidence of the husband, and was not mentioned to Prof. Dalton until after the child was born. As such, it might be rejected as one of those instances in which the explanation is a statement following a knowledge of the deformity. Still, we ourselves know the husband to be an intelligent man, and believe that his statement of the circumstances is reliable.

Union of the Male with the Female Element of Generation.—The first important step in our positive knowledge of the mechanism of fecundation was the discovery of the spermatozoids, in 1677, to which we have already referred; the second was the demonstration, by Spallanzani, in his experiments upon artificial fecundation, that when the seminal fluid is carefully filtered, the liquid which passes through has no fecundating properties, the male element remaining on the filter; and the third was the demonstration of the presence of spermatozoids within the vitelline membrane, showing that fecundation consists in a direct union of the male with the female element.

Spallanzani filtered the seminal fluid of frogs, and found that its fecundating properties were diminished in proportion as the filtration was thorough, and that the fluid was inactive when filtered through six or seven papers; but, when the substance remaining on the filters was taken and mixed with water, this readily fecundated ova. Spallanzani also made a number of interesting experiments upon artificial fecundation in mammals. In connection with Prof. Rossi, he injected seminal fluid from a dog into a bitch in heat, on

[1] Communication from Prof. Dalton.

four occasions, at intervals of one or two days. Sixty-two days after the first injection, the bitch had four pups, which resembled the male as well as the female. With the semen of the same dog, he attempted to fecundate two cats in heat, but was unsuccessful, although the experiments were made in the same way as with the bitch.[1] It is not easy to explain why the spermatozoids from the dog could not penetrate the vitelline membrane and fecundate the ova of the cat, but this seems to be impossible in animals so widely different.

As to the mechanism of the penetration of spermatozoids to the vitellus, we can only refer to the micropyle discovered in the ova of fishes and mollusks, which we have already described.[2] In the ova of the Nephelis, a small species of leech, Robin has seen spermatozoids, to the number of several hundreds, penetrate the vitelline membrane, always at one point, continuing their movements upon the surface of the vitellus. "Almost always, when the penetration has ceased, a bundle of spermatozoids are arrested in the micropyle."[3] We had an opportunity of witnessing a demonstration of these phenomena by Prof. Robin, in 1861, in the ova of the Limnæus stagnalis, and actually saw a spermatozoid half-way through the vitelline membrane. According to numerous direct observations, the spermatozoids move actively around the ovum, collect toward a certain point, and there penetrate the vitelline membrane. Coste, and many other observers, whom it is unnecessary to quote, have seen the spermatozoids within the vitelline membrane, in the ovum of the rabbit;[4] and, more recently, Weil has seen spermatozoids wedged in the substance of the zona pellucida, has added blood to the specimen under observation, and has restored the movements of the spermatozoids while in this position. He has also seen,

[1] Spallanzani, *Expériences pour servir à l'histoire de la génération*, Pavie, 1797, p. 310, *et seq.*

[2] See page 290.

[3] Robin, *Mémoire sur les phénomènes qui se passent dans l'ovule.—Journal de la physiologie*, Paris, 1862, tome v., p. 80.

[4] Coste, *Développement des corps organisés*, Paris, 1859, tome ii., p. 108.

in some instances, perfectly-formed spermatozoids in the very substance of the vitellus.[1]

The following very interesting experiment by Lott has a certain amount of bearing upon the question of the penetration of spermatozoids through the vitelline membrane. Lott made a little bag of the cæcum of the sheep, moistened the membrane with a weak saline solution, introduced ten to twelve drops of ejaculated semen, and, having closed the bag securely, placed it in a vessel containing the same saline solution. In ten minutes, he drew out the bag and found, in the exterior liquid, a number of motionless spermatozoids. This observation he often repeated, with similar results; showing that the spermatozoids had actually passed through this delicate animal membrane.[2] How far this explains the passage of spermatozoids through the vitelline membrane, it is difficult to say; but the results are certainly curious and somewhat startling.

All direct observations on the lower orders of animals have shown that several spermatozoids are necessary for the fecundation of a single ovum; but we have no definite idea of the number required in mammals, much less in the human subject. Nor do we know what becomes of the spermatozoids after they have come in contact with the vitellus. All that we can say upon this point is, that there is probably a molecular union between the two generative elements, soon to be followed by the remarkable series of changes involved in the first processes of development.

[1] WEIL, *Beiträge zur Kentniss der Befruchtung und Entwicklung des Kaninchenceies.—Medizinische Jahrbücher*, Wien, 1873, S. 18, *et seq.*

[2] LOTT, *Zur Anatomie und Physiologie des Cervix Uteri*, Erlangen, 1872, S. 40.

CHAPTER XV.

SEGMENTATION OF THE VITELLUS AND FORMATION OF THE MEMBRANES AND PLACENTA.

Deformation and gyration of the vitellus—Polar globule—Vitelline nucleus—Segmentation of the vitellus—Primitive trace of the embryon—Blastodermic layers—Formation of the membranes—Formation of the amnion—Amniotic fluid—Formation of the umbilical vesicle—Formation of the allantois and the permanent chorion—Umbilical cord—Membranæ deciduæ—Development and structure of the placenta—Structure of the fully-developed placenta—Blood-vessels of the placenta.

As we have seen in the preceding chapter, it is probable that the ovum is fecundated, either just as it enters the Fallopian tube or in the dilated portion near the ovary. As it passes down the tube, whether it be or be not fecundated, it becomes covered with an albuminous layer. This layer probably serves to protect the fecundated ovum, and, when the spermatozoids do not penetrate the vitelline membrane near the ovary, presents an obstacle to their passage. Shortly after fecundation, the germinal vesicle disappears; but this occurs in ova that have not been fecundated. Soon after ovulation, also, the vitellus gradually withdraws itself from certain portions of the vitelline membrane, or becomes deformed, and then often rotates upon itself; a phenomenon which has long been observed in the ova of some of the lowest orders of animals, but which was seen by Bischoff in the ova of rabbits, and was thought by him to be due to the movements of cilia upon the surface of the vitellus.[1] The presence of cilia in this situation, however, has not been con-

[1] **Bischoff**, ***Traité du développement de l'homme et des mammifères.—Encyclopédie anatomique***, **Paris, 1843, tome viii., p. 598.**

firmed by more recent observations. The deformation and gyration of the vitellus have been observed in ova before fecundation, and have nothing to do with the process of development. They are of the class of movements called amœboid.

After the penetration of spermatozoids and their union with the vitellus, at least in many of the lower orders of animals, the appearance of the vitellus undergoes a remarkable change, by which ova that are about to pass through the first processes of development may be readily distinguished from those which have not been fecundated. This change consists in an enlargement of the granules and their more complete separation from the clear substance of the vitellus. The granules then refract light more strongly than before, so that the fecundated ova are distinctly brighter than the others.[1] This is the first appearance that is distinctive of fecundation.

Polar Globule.—The next process observed in the ovum is the separation from the vitellus of a comparatively clear, rounded mass, called by Robin the polar globule. This body had been observed before by various anatomists and described under different names. The exact mode of its formation has been studied by Robin in some of the lower orders of animals.[2] We shall describe briefly this process as it was demonstrated to us by Robin in the ova of the Limnæus stagnalis, in 1861, the description being taken from notes made at that time:

Five hours after the entrance of the spermatozoids, we see a little elevation at one point in the vitellus. This is the beginning of the polar globule. It increases in size gradually, and becomes constricted at its base, until it is attached to the vitellus by a little pedicle. There is then, usually, a second globule formed just behind the first, in the same man-

[1] Robin, *Mémoire sur les phénomènes qui se passent dans l'ovule avant la segmentation du vitellus.—Journal de la physiologie*, Paris, 1862, tome v., p. 108.

[2] Robin, *Mémoire sur les globules polaires de l'ovule.—Journal de la physiologie*, Paris, 1862, tome v., p. 149, *et seq.*

ner; and sometimes a third makes its appearance. As soon as the globules are perfectly formed, they all become detached from the vitellus, but remain adherent to each other, gradually fusing to form a single rounded, very faintly granular mass; and it is opposite this globule that the first furrow of segmentation of the vitellus is observed. The complete formation of the polar globules and their fusion into one occupy three hours. It is probable that the polar globule is formed in the mammalia in the manner above indicated. Weil has lately described, in the fecundated ovum of the rabbit, before segmentation of the vitellus, a body which is undoubtedly analogous to this globule.[1] Sometimes the polar globule is formed in ova that have not been fecundated.

Vitelline Nucleus.—A short time after the complete formation of the polar globule, the germinal vesicle having disappeared, the deformed vitellus resumes its original rounded appearance, and fills again the cavity of the vitelline membrane. At this time, the extreme periphery of the vitellus becomes clearer; the granules collect in a large zone around the centre, and, in the centre itself, a clear, rounded body makes its appearance, which is called the nucleus of the vitellus. This mass is viscid, amorphous, without granules, and is entirely different from the germinal vesicle, having no nucleolus at first, a nucleolus, however, appearing in the nuclei which result from its segmentation. The formation of the nucleus of the vitellus is a positive evidence of fecundation. It appears from fifteen to thirty hours after fecundation.[2]

Segmentation of the Vitellus.—Almost immediately following the phenomena we have just described, the vitellus begins to undergo the remarkable process of segmentation, by which it is divided into numerous small cells. This pro-

[1] WEIL, *Beiträge zur Kentniss der Befruchtung und Entwicklung des Kaninchenseies.—Medizinische Jahrbücher*, Wien, 1873, S. 24.

[2] ROBIN, *Note sur la production du noyau vitellin.—Journal de la physiologie*, Paris, 1862, tome v., p. 314.

cess may take place to a limited extent in non-fecundated ova; but in this case the cells soon disappear, as the disintegration of the ovum advances. The true segmentation of the vitellus, however, results in the formation of what are called the blastodermic cells. As segmentation has been studied in the inferior animals, there appears first a furrow in the vitellus, at the site of the polar globule; and there is then a furrow on the opposite side, both deepening until the entire vitellus is divided into two globes. These are at first spherical; but they soon become flattened upon each other into two hemispheres. There is then a similar division into four, another into eight, and so on, until the entire vitellus is divided into numerous cells, each with a clear nucleus resulting from the segmentation of the original nucleus of the vitellus. It is probable that, at first, the cells of the vitellus have no membrane; but a membrane is soon formed, a nucleolus appears and the cells are perfect.

Most of the phenomena of segmentation have been observed in the lower orders of animals; but there can be no doubt that analogous processes take place in the human ovum. In the rabbit, Weil observed, forty-five and a half hours after copulation, an ovum, with sixteen segmentations, situated in the lower third of the Fallopian tube. Ninety-four hours after copulation, he observed an ovum, with a delicate mosaic appearance, presenting a small, rounded eminence on its surface.[1]

It is impossible to say how long the process of segmentation continues in the human ovum. It is stated that it is completed in rabbits in a few days, and in dogs, that it occupies more than eight days.[2] When the cells of the blastoderm are completely formed, they present a polygonal appearance as they are pressed against the vitelline membrane, their inner surface being rounded. The ovum then contains, within the external layer of cells, a small quantity of liquid. It is

[1] WEIL, *loc. cit.*, S. 26.

[2] HERMANN, *Grundiss der Physiologie*, Berlin, 1870, S. 469.

probably in this condition that the ovum passes from the Fallopian tube into the uterus, at about the eighth day after fecundation.[1]

Primitive Trace of the Embryon.—The cells formed by the segmentation of the vitellus, after this process is completed, are arranged in the form of a membrane, the blastodermic membrane, which is farther subdivided, as development advances, into layers, which will be fully described hereafter. The albuminous covering which the ovum has received in the upper part of the Fallopian tube gradually liquefies and penetrates the vitelline membrane, furnishing, it is thought, matter for the nourishment and development of the vitellus. In the Fallopian tube, indeed, the adventitious albuminous covering of the ovum presents an analogy to the albuminous coverings which the eggs of oviparous animals receive in the oviducts; with the difference that this albuminous matter is almost the sole source of nourishment in the latter, and exists in large quantity, while, in viviparous animals, the quantity is small, is generally consumed as the ovum passes into the uterus, and, in the uterus, the ovum forms attachments to and draws its nourishment from the vascular system of the mother.

At the period when the fecundated ovum enters the uterus, it has increased in size about five times.[2] It is then composed of an external covering, the vitelline membrane, with a cellular membrane internal to this, the blastodermic membrane, and a certain amount of liquid in its interior.

Soon after the formation of the single blastodermic membrane, at a certain point on its surface, there appears a rounded elevation, or heap of smaller cells, forming a distinct spot, called the embryonic spot. As development advances, this spot becomes elongated and oval. It is then surrounded by a clear, oval area, called the area pellucida, and the area pellucida is itself surrounded by a zone of cells,

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 841. [2] Ibid.

more granular and darker than the rest of the blastoderm. The elongated line thus formed and surrounded by the area pellucida is called the primitive trace.

Almost all writers have regarded the primitive trace as the seat of the development of the spinal column of the embryon; but some doubt has been thrown upon this point by the observations of Dursy, in 1866, quoted and recently confirmed by Balfour. According to these observations, which were made upon the chick, the primitive trace, or primitive groove, is a temporary structure, and has nothing to do with the development of the neural canal. After this groove is formed, Balfour states that there appears in front of, but not continuous with it, a new fold and a groove leading from it. This is the "head-fold," and the groove is the true medullary groove, which is subsequently developed into the neural canal.[1] If we adopt this view, and the difference is not very important, we simply substitute the new trace, the seat of the development of the neural canal, for the original primitive trace, which is temporary. It is probable that embryologists have heretofore noted the so-called primitive trace and studied subsequently the development of the true medullary groove, supposing that they were identical structures in different stages of formation, not observing that the first trace disappears.

Blastodermic Layers.—Shortly after the appearance of the primitive trace, the blastodermic cells, which are at first arranged so as to form a single membrane, separate into layers. These layers have been differently described by various observers, and there is some uncertainty with re-

[1] BALFOUR, *On the Disappearance of the Primitive Groove in the Embryo Chick.—Quarterly Journal of Microscopical Science*, London, 1873, New Series, No. li., p. 276, *et seq.*

The mutual relations of the primitive trace and the medullary groove in the chick are figured in the elaborate work of His. (*Untersuchungen über die erste Anlage des Wirbelthierleibes. Die erste Entwicklung des Hühnchens im Ei*, Leipzig, 1868, Taf. xii., Fig. 14.)

gard to the application of direct researches made upon the chick, in which most of these early processes of development have been studied, to the mammalia and the human subject. We shall endeavor to describe the different layers in as simple a manner as is consistent with our positive knowledge, omitting all points that are unsettled or seem to be of minor importance.

The blastodermic cells, resulting originally from the segmentation of the vitellus, are first apparently split into two layers, which may be termed the external and the internal blastodermic membranes. According to the most recent observations, the main portion of the external layer, sometimes called the serous layer, simply forms a temporary investment for the rest of the vitellus and is not developed into any part of the embryon. The internal layer, called the mucous layer, is developed into nothing but the epithelial lining of the alimentary canal. There is a thickening of both of these layers at the line of development of the cerebro-spinal system, with a furrow, which is finally enclosed by an elevation of the ridges and their union posteriorly, forming the canal for the spinal cord.

As the spinal canal is thus developed, a new layer is formed, by a genesis of cells from the internal surface of the original external layer and the opposite surface of the internal, or mucous layer. This layer of new cells may be termed the intermediate layer; and it is from this that nearly all the parts of the embryon are developed.

To summarize the development of the layers just mentioned, we may state that the external layer is a temporary structure; the internal layer is very thin, and is for the development of the epithelial lining of the alimentary canal; the most important structure is a thick layer of cells, developed from the opposite surfaces of the external and the internal layer, and situated between them, called the intermediate layer; and it is from these cells that the greatest part of the embryon is formed.

Formation of the Membranes.

The brief description we have just given of the formation of the blastodermic layers seemed necessary as an introduction to the study of the membranes; and we shall defer, for the present, the description of their development into the different parts of the embryon.

In the mammalia, a portion of the blastoderm is developed into membranes, by which a communication and union are established between the ovum and the mucous membrane of the uterus. From the ovum, are developed two membranes, one non-vascular, the amnion, and another vascular, the allantois. From the mucous membrane of the uterus, are developed the two layers of the decidua. At a certain part of the uterus, a vascular connection is established between the mucous membrane and the allantois, and the union of these two structures forms the placenta. The fœtal portion of the placenta is connected with the fœtus by the vessels of the umbilical cord; and the maternal portion is connected with the great uterine sinuses. Development takes place from material supplied to the fœtus by the blood of the mother.

The external covering of the ovum, during the first stage of its development, is the vitelline membrane. According to Coste, as the ovum is received into the uterus, the vitelline membrane develops upon its surface little villosities, which are non-vascular, and formed of amorphous matter with granules. These are the first villosities of the ovum, and they assist in fixing the egg in the uterine cavity. They are not permanent, do not become developed into the vascular villosities of the chorion, and disappear as the true membranes of the embryon are developed from the blastodermic layers.[1] It is probable that the vitelline membrane disappears about the fourth or fifth day, when it is replaced by the amnion.

Formation of the Amnion.[2]—As the ovum advances in its

[1] Coste, *Développement des corps organisés*, Paris, 1847, tome i., p. 82.

[2] In the literature pertaining to the subject of development, there is no de-

development, it is observed that a portion of the blastoderm becomes thickened, to form the first trace of the embryon. At this portion, where the body of the embryon subsequently makes its appearance, as we have already seen, we have the external layer, the internal layer, and a thick, intermediate layer of cells, developed from the opposite surfaces of the external and the internal layer, called the middle layer. At nearly the time when this thickening begins, a fold of the external layer makes its appearance, surrounding the thickened portion, and most prominent at the cephalic and the caudal extremity of the furrow for the neural canal. This fold increases in extent as development advances, passes over the dorsal surface of the embryon, and finally meets so as to enclose the embryon completely. We can readily figure to ourselves this process and understand how, at a certain period of the development of the amnion, this membrane consists of an external layer, formed of the external layer of the fold, and an internal layer; the point of union of the two layers, or the point of meeting of the fold, being marked by a membranous septum. An illustration of this mode of formation of the two layers of the amnion is afforded by an observation by Allen Thomson, made on an embryon of about fifteen days, in which there was a portion of membrane extending from the internal amniotic fold to the external covering of the ovum.[1]

scription of the mode of formation of the membranes so clear and exact as that given by Dalton, in his Treatise on Physiology. In our account of these processes, we shall follow in the main this description. (DALTON, *Human Physiology*, Philadelphia, 1871, p. 619, *et seq.*)

[1] ALLEN THOMSON, *Contributions to the History and Structure of the Human Ovum*, etc.—*Edinburgh Medical and Surgical Journal*, 1839, vol. iii., p. 182. This observation is quoted by Longet as showing the mechanism of formation of the amnion (*Traité de physiologie*, Paris, 1869, tome iii., p. 844); but the statement in the original paper by Allen Thomson is rather indefinite. Alluding to "a portion of fine membrane which adhered to the notch between the fœtus and yolk at the cephalic extremity," he says: "I am inclined to believe that this piece of membrane may be a part of the cephalic fold of the serous layer of the germinal membrane which forms the amnios." The ovum was not examined until after it had been in alcohol for several days.

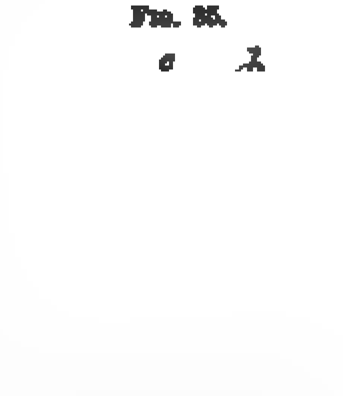
The two amniotic layers are formed in the way that we have just described, and a complete separation finally takes place, by a disappearance of the septum formed by the meeting of the folds over the back of the embryon. According to Longet, this process occupies four or five days in the human ovum;[1] though the observation by Allen Thomson shows that the complete separation of the two layers occurs much later. The point where the folds meet is called the amniotic umbilicus. When the amnion is thus completely formed, the vitelline membrane has been encroached upon by the external amniotic layer and disappears, leaving this layer of the amnion as the external covering of the ovum. At this time, there is a growth of villosities upon the surface of the external amniotic layer, which, like the villosities of the vitelline membrane, are not vascular.

FIG. 34.

Fecundated egg.—*a*, umbilical vesicle; *b*, amniotic cavity; *c*, allantois. (DALTON, *Human Physiology*, Philadelphia, 1871, p. 621.)

Soon after the development of the amnion, the allantois is formed. This membrane is vascular, encroaches upon and takes the place of the external amniotic membrane, becomes villous, and its villosities take the place of those of the amnion. Over a certain portion of the membrane, the villosities are permanent. The mode of development of the amnion, as we have described it, was discovered by Von Baer,[2] and is illustrated by the diagrammatic Figs. 34 and 35. These figures show the formation of the amnion, the

FIG. 35.



Fecundated egg, with allantois nearly complete.—*a*, inner lamina of amniotic fold; *b*, outer lamina of ditto; *c*, point where the amniotic folds come in contact. The allantois is seen penetrating between the inner and outer laminæ of the amniotic folds. (DALTON, *Human Physiology*, Philadelphia, 1871, p. 621.)

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 844.

[2] VON BAER, *Ueber Entwickelungsgeschichte der Thiere*, Königsberg, 1837, Zweite Theil, S. 192.

umbilical vesicle, and the allantois. The last two structures are not derived from the external blastodermic layer, and will be described farther on, after we have studied the full development of the amnion and its relations.

When the allantois has become the chorion, or the external membrane of the ovum, having taken the place of the external layer of the amnion, the structures of the ovum are the following: 1. The chorion, formed of the two layers of the allantois, derived from the internal blastodermic membrane, and penetrated by blood-vessels. 2. The umbilical cord, which connects the embryon with the placental portion of the chorion, and the umbilical vesicle, formed from the same layers as the allantois. 3. The amnion, which is the internal layer of the amniotic fold, persisting throughout the whole of fœtal life. 4. The embryon itself.

During the early stages of development of the umbilical vesicle and the allantois, the internal amniotic layer, or the true amniotic membrane, is closely applied to the surface of the embryon, and is continuous with the epidermis at the umbilicus. It is then separated from the allantois by a layer of gelatinous matter; and in this layer, between the amnion and the allantois, is embedded the umbilical vesicle. At this time, the umbilical cord is short and not twisted. As development advances, however, the inter-membranous gelatinous matter gradually disappears; the cavity of the amnion is enlarged by the production of a liquid between its internal surface and the embryon; and, at about the end of the fourth month, the amnion comes in contact with the internal surface of the chorion. At this time, the embryon floats, as it were, in the amniotic cavity, surrounded by the amniotic fluid. The amnion forms a lining membrane for the chorion; by its gradual enlargement it has formed a covering for the umbilical cord; and, between it and the cord, is the atrophied umbilical vesicle. The amnion then resembles a serous membrane, except that it is non-vascular. It is lined by a single layer of pale, delicate cells of pavement-epithelium,

which contain a few fine, fatty granulations. At term, the amnion adheres to the chorion, though it may be separated, with a little care, as a distinct membrane, and may be stripped from the cord. From its arrangement and from the absence of blood-vessels, it is evident that this membrane is simply for the protection of the fœtus and is not directly concerned in its nutrition and development.

The gelatinous mass referred to above, situated, during the early periods of intra-uterine life, between the amnion and the chorion, presents a semifluid consistence, and is marked by the presence of numerous very delicate, interlacing fibres of young connective tissue and fine, grayish granulations scattered through its substance. These fibres gradually develop as the quantity of gelatinous matter diminishes and the amnion approaches the chorion, until, finally, it forms a rather soft, reticulated layer, which was described by Bischoff, under the name of the membrana media.[1]

Amniotic Fluid.—The process of enlargement of the amnion shows that the amniotic fluid gradually increases in quantity as the development of the fœtus progresses. At term, the entire quantity is variable, being rarely more than two pints or less than one pint.[2] In the early periods of utero-gestation, it is clear, slightly yellowish or greenish, and perfectly liquid. Toward the sixth month, its color is more pronounced, and it becomes slightly mucilaginous. Its reaction is usually neutral or faintly alkaline, though sometimes it is feebly acid in the latest periods. It sometimes contains a small quantity of albumen, as determined by heat and nitric acid; and there is generally a gelatinous precipitate on the addition of acetic acid. The following table, compiled by Robin, gives its chemical composition:

[1] Bischoff, *Traité du développement.—Encyclopédie anatomique*, Paris, 1843, tome viii., p. 157.

Robin, *Mémoire sur la structure intime de la vésicule ombilicale.—Journal de la physiologie*, Paris, 1861, tome iv., p. 306.

[2] Robin, *Leçons sur les humeurs*, Paris, 1867, p. 779.

Composition of the Amniotic Fluid.[1]

Water	991·00 to 975·00
Albumen and mucosine	0·82 " 10·77
Urea	2·00 " 3·50
Creatine and creatinine (Scherer, Robin and Verdeil)	not estimated
Lactate of soda (Vogt, Regnauld)	a trace
Fatty matters (Rees, Mack)	0·13 to 1·25
Glucose (Cl. Bernard)	not estimated
Chloride of sodium and chloride of potassium	2·40 to 5·95
Chloride of calcium	a trace
Carbonate of soda	a trace
Sulphate of soda	a trace
Sulphate of potassa (Rees)	a trace
Calcareous and magnesian phosphates and sulphates	1·14 to 1·72

The presence of certain of the urinary constituents in the amniotic fluid has led to the view that the urine of the fœtus is discharged, in greater or less quantity, into the amniotic cavity. Bernard, who is quoted in the above table as having determined the presence of sugar in the amniotic fluid, has shown that, in animals with a multiple placenta, the amnion has a glycogenic function during the early part of intra-uterine existence.[2]

With regard to the origin of the amniotic fluid, it is impossible to say how much of it is derived from the general surface of the fœtus, how much from the urine, and how much from the amnion itself, by transudation from the vascular structures beneath this membrane. The quantity is apparently too great, especially in the early months, to be derived entirely from the urine of the fœtus, and there is probably an exudation from the general surface of the fœtus and from the membranes. After the third month, the sebaceous secretion from the skin of the fœtus prevents the absorption of any of the liquid.

An important property of the amniotic fluid is that of resisting putrefaction and of preserving dead tissues. It is

[1] ROBIN, *Leçons sur les humeurs*, Paris, 1867, p. 782.

[2] See vol. iii., Secretion, p. 322.

stated by Robin to be the best fluid for the preservation of the embryonic tissues, when it is desired to keep them for examination.

Formation of the Umbilical Vesicle.—As the visceral plates, which will be described hereafter, close over the front of the embryon, that portion of the blastoderm from which the intestinal canal is developed presents a vesicle, which is cut off, as it were, from the abdominal cavity, but still communicates freely with the intestine. This is the umbilical vesicle. On its surface, is a rich plexus of blood-vessels; and this is a very important organ in birds and in many of the lower orders of animals. In the human subject and in mammals, however, the umbilical vesicle is not so important, as nutrition is effected by means of vascular connections between the chorion and the uterus. The vesicle becomes gradually removed farther and farther from the embryon, as development advances, by the elongation of its pedicle, and is compressed between the amnion and the chorion as the former membrane becomes distended.

When the vesicle is formed, in the way which we have indicated, it receives two arteries from the two aortæ, and the blood is returned to the embryon by two veins, which open into the vestibule of the heart. These are called the omphalo-mesenteric vessels. At about the fortieth day, one artery and one vein disappear, and, soon after, all vascular connection with the embryon is abolished. At first there is a canal of communication with the intestine, called the omphalo-mesenteric canal. This is gradually obliterated, and closes at the thirtieth or the thirty-fifth day. The point of communication of the vesicle with the intestine is called the intestinal umbilicus; and, early in the process of development, there is here a true hernia of a loop of intestine. The umbilical vesicle remains as a tolerably prominent structure as late as the fourth or fifth month, but it may often be discovered at the end of pregnancy.

According to Robin, the umbilical vesicle has three coats; an external, smooth membrane, formed of connective tissue, a middle layer of transparent, polyhedric cells, and an internal layer of spheroidal cells. The membrane, composed of these layers, encloses a pulpy mass, composed of a liquid, containing cells and yellowish granulations.[1]

Formation of the Allantois and the Permanent Chorion.—During the early stages of development of the umbilical vesicle, and while it is being shut off from the intestine, there appears an elevation at the posterior portion of the intestine, which rapidly increases in extent, until it forms a membrane of two layers, which is situated between the internal and the external layer of the amnion. This membrane becomes vascular early in the progress of its development, increases in size quite rapidly, and finally completely encloses the internal layer of the amnion and the embryon, the gelatinous mass already described being situated between it and the internal amniotic layer before this membrane becomes enlarged. While the formation of the two layers of the allantois is quite distinct in certain of the lower orders of animals, in the human subject and in mammals, it is not so easily observed; still, as was first shown by Coste,[2] there can be no doubt as to the mechanism of its formation, even in the human ovum. Here, however, the allantois soon becomes a single membrane, the two original layers of which cannot be separated from each other. The process of the development of the allantois is shown in the diagrammatic figures 34, 35, and 36.

It is the vascularity of the allantois which causes the rapid development by which it invades and finally supersedes the external layer of the amnion, becoming the permanent chorion, or external membrane of the ovum. At first there are two arteries extending into this membrane from the lower

[1] Robin, *Mémoire sur la structure intime de la vésicule ombilicale.—Journal de la physiologie*, Paris, 1861, tome iv., pp. 308, 314.

[2] Coste, *Embryogénie comparée*, Paris, 1837, tome i., p. 281, *et seq.*

portion of the aorta, and two veins. The two arteries persist and form the two arteries of the umbilical cord, coming from the internal iliac arteries of the fœtus; and the two veins are reduced to one, the umbilical vein, which returns the blood from the placenta to the fœtus. These vessels are connected with the permanent vascular tufts of the chorion.

Longet states, as the result of a study of the specimens in the College of France, prepared by Coste, that the development of the allantois cannot be well observed in human ova before the fifteenth or the twenty-fifth day.[1] We have already noted the formation of villosities, first upon the vitelline membrane, and next upon the external amniotic membrane, and we have seen that both of these membranes are temporary structures. As the vascular allantois encroaches upon the external amniotic layer, the villosities become vascular; and, when the allantois becomes the permanent chorion, it is marked by a multitude of compound villi over its entire surface, which give the ovum a shaggy appearance.

FIG. 86.

Fecundated egg, with allantois fully formed. — *a*, umbilical vesicle; *b*, amnion; *c*, allantois. (DALTON, *Human Physiology*, Philadelphia, 1871, p. 622.)

It is difficult to say whether new villi appear upon the allantois, or whether the villi of the amnion are penetrated by the vessels of the allantois; but it is certain that the true or permanent chorion presents upon its surface vascular villi. As the ovum enlarges, over a certain area surrounding the point of attachment of the pedicle which connects it with the embryon, the villi are developed more rapidly than over the rest of the surface. Indeed, as the egg becomes larger and larger, the villi of the surface outside of this area become more and more scanty, lose their vascularity, and finally disappear. That portion upon which the villi persist and increase in length and in the number of their branches is

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 849.

destined to form connections with the mucous membrane of the uterus, and constitutes the fœtal portion of the placenta. According to Dalton, this change begins at about the end of the second month, and the placenta becomes distinctly limited at about the end of the third month.[1]

It must be remembered that, as the changes progress which result in the formation of the permanent chorion and the limitation of the fœtal portion of the placenta, the formation of the umbilical vesicle and the enlargement of the amnion are also going on. The amnion is gradually becoming distended by the increase in the quantity of amniotic fluid; it reaches the internal surface of the chorion at about the end of the fourth month, extends over the umbilical cord to form its external covering, including the cord of the umbilical vesicle, and the umbilical vesicle itself lies in the gelatinous matter between the two membranes.

At about the beginning of the fifth month, then, the ovum is constituted as follows:

The fœtus floats freely in the amniotic fluid, attached to the placenta by the umbilical cord; the chorion presents a highly vascular, thickened, and villous portion, the fœtal portion of the placenta; the rest of the chorion is a simple membrane, without villi and without blood-vessels; the amnion lines the internal surface of the chorion, and also forms the external covering of the umbilical cord; the umbilical vesicle has become atrophied and has lost its vascularity; the hernia at the point of connection of the umbilical vesicle with the intestine of the fœtus has closed; finally, the fœtus has undergone a considerable degree of development.

It now remains for us to study the structure of the umbilical cord, the membranes formed from the mucous membrane of the uterus, or the membranæ deciduæ, and the mode of development and the structure of the placenta.

Umbilical Cord.—From the description we have given of

[1] DALTON, *Human Physiology*, Philadelphia, 1871, pp. 632, 633.

the mode of development of the chorion and the amnion, it is evident that the umbilical cord is nothing more than the pedicle which connects the embryon with that portion of the chorion which enters into the structure of the placenta. It is, indeed, a process of the allantois, in which the vessels eventually become the most important structures. The cord is distinct at about the end of the first month; and, as development advances, the vessels consist of two arteries coming from the body of the fœtus, which are usually twisted from left to right around the single umbilical vein. In addition to the spiral turns of the arteries around the veins, the entire cord may be more or less twisted, probably from the movements of the fœtus.

The fully-developed cord extends from the umbilicus of the fœtus to the central portion of the placenta, in which its insertion is usually oblique; though it may be inserted at other points, and even outside of the border of the placenta, its vessels penetrating this organ from the side. Its usual length, which varies very considerably, is about twenty inches. It has been observed as long as sixty, and as short as seven inches.[1] When the cord is very long, it sometimes presents knots, or may be wound around the neck, the body, or any of the members of the fœtus; and this can only be accounted for by the movements of the fœtus *in utero*.

The external covering of the cord is a process of the amnion, which, as it extends over the vessels, includes a gelatinous substance, the gelatine of Wharton, which surrounds the vessels, and protects them from compression. This gelatinous substance is identical with the so-called membrana intermedia, or the substance included between the amnion and the chorion. The entire cord, covered with the gelatine of Wharton and the amnion, is usually about the size of the little finger. According to Robin, the normal cord will sustain a weight of from ten pounds and ten ounces

[1] VROLIK, *Cyclopædia of Anatomy and Physiology*, London, 1849–1852, vol. iv., part ii., p. 947, Article, *Teratology*.

to twelve pounds and twelve ounces avoirdupois.[1] As the amniotic fluid accumulates and distends the amniotic membrane, it becomes more and more closely applied to the cord. This pressure extends from the placental attachment of the cord toward the fœtus, and gradually forces into the abdomen of the fœtus the loop of intestine, which, in the early periods of intra-uterine life, forms an umbilical hernia.

It is generally stated by writers upon embryology that the vessels of the cord present no valves; but recent observations by Berger have demonstrated the presence of semilunar folds, both in the vein and in the arteries. In the historical account of this subject, given by Berger, it is stated that many of the older writers described these folds more or less accurately, and that they were observed more recently by Hyrtl. Berger rejects the term valves, as applied to the semilunar folds which he has observed, particularly as regards those found in the umbilical vein. They are simple inversions of the walls of the vessels; and they do not exist in pairs, nor do they seem to influence the current of blood. In the arteries, these folds are situated at intervals of from half an inch to two inches, and are more abundant where the vessels are very contorted. In the vein, the folds are most abundant near the placenta; they are very irregularly placed, and, in a length of four inches, fifteen folds were found. It is not apparent that these folds have any physiological importance.[2]

As the allantois is developed, it presents, in the early stages of its formation, three portions: an external portion, which becomes the chorion, an internal portion, enclosed in the body of the embryon, and an intermediate portion. The intermediate portion, as we have seen, becomes the umbilical cord. As the umbilicus of the fœtus closes around the cord,

[1] LITTRÉ ET ROBIN, *Dictionnaire de médecine*, Paris, 1873, Article, *Ombilical*.

[2] BERGER, *Recherches sur la conformation intérieure de la veine et des artères ombilicales.—Archives de physiologie*, Paris, 1871–1872, tome iv., p. 551, *et seq.*

it shuts off a portion of the allantois contained in the abdominal cavity, which becomes the urinary bladder; but there is a temporary communication between the internal portion and the lower portion of the cord, which is called the urachus. This is generally obliterated before birth, and is reduced to the condition of an impervious cord; but it may persist during the whole of intra-uterine life, in the form of a narrow canal, extending from the bladder to the umbilicus, which is closed soon after birth.

Membranæ Deciduæ.—In addition to the two membranes connected with the fœtus, there are two membranes formed from the mucous membrane of the uterus, which are derived from the mother, and which serve still farther to protect the ovum. The chorion, as we have just seen, is for the protection of the fœtus; but a portion of this membrane, about one-third of its surface, becomes closely united with a corresponding portion of the uterine mucous membrane, to form the placenta. This organ, which serves for the nutrition of the fœtus, will be described by itself; but, before we can thoroughly comprehend its structure and the process of its development, we must study carefully the formation of the membranæ deciduæ.[1]

As the fecundated ovum descends into the uterus, it is usually invested with a shaggy covering, which is either the permanent chorion or one of the membranes which invests the ovum previous to the complete development of the allantois. At this time, the mucous membrane of the uterus has undergone certain changes by which it is prepared for the reception of the ovum. The changes which this membrane

[1] The first correct account of the decidua was given by William Hunter, who recognized this as a modification of the uterine mucous membrane, and gave it the name it now bears. The engravings illustrating the anatomy of the gravid uterus, with the membranes, were published in 1774. A full account of the decidua is in a posthumous publication, edited by Dr. Rigby. (Hunter, *An Anatomical Description of the Human Gravid Uterus and its Contents*, London, 1843, p. 46, *et seq.*)

undergoes in menstruation have already been studied.[1] It has been seen that, during an ordinary menstrual period, the membrane has been increased three or four times in thickness and has become more or less rugous. Without being able to state from positive observation the character of the first changes in the uterine mucous membrane preceding the descent of the fecundated ovum—for the opportunities for direct inspection of these parts after fecundation and before the arrival of the ovum are not frequent—it is almost certain that this hypertrophy occurs and progresses. One of the most favorable occasions for observing these early changes in the human subject lately presented itself, and the appearances were minutely described by Reichert. In this case, the ovum was lenticular, measuring nearly one-fourth of an inch in its long, and about one-sixth of an inch in its short diameter. It was covered with simple, empty, cylindrical villi, and was estimated to be at from the twelfth to the thirteenth day of its development, dating from fecundation. It was enclosed in the decidua reflexa, and it was thought that this had been accomplished from twenty-four to forty-eight hours before the death of the mother.

According to Reichert, the thickening of the mucous membrane of the uterus, which occurs at each menstrual period, in case the ovum be not fecundated, is relieved by a flow of blood and disappears; but, if fecundation take place, the membrane continues to hypertrophy and to prepare itself to enclose the ovum. In this process, when an ovum has been fecundated, there are formed, upon the surface of the mucous membrane, little elevations, or islands, provided with primary and secondary papillæ, everywhere except at their borders, where the membrane is smooth and presents the enlarged orifices of the uterine follicles. The ovum observed by Reichert was found embedded in the parenchyma of one of these islands; and, as it was detached, several villi were drawn immediately out from the uterine tubules.

[1] See page 306.

It is now well known that the mucous membrane lining the gravid uterus forms what has been called the decidua vera, and that a portion is reflected over the ovum, to form the decidua reflexa. Reichert is of the opinion that the view entertained by most observers, that the fecundated ovum lodges itself in one of the furrows of the hypertrophied membrane and is finally enclosed by an elevation of the walls of the furrow, cannot be sustained. He thinks that the ovum first becomes attached to one of the "islands;" at the point of attachment, the island does not increase in size as rapidly as at other portions, so that the ovum rests in a cup-shaped depression; finally, a growth takes place from the margin of this depression, which extends around and encloses the ovum, presenting a spot where the final closure takes place, called the decidual umbilicus.[1]

We have given the recent views of Reichert thus fully, for the reason that they are based upon the study of a remarkably young ovum, and appear to be more exact and definite than any observation hitherto recorded; and we shall adopt this description as representing the early stages of the formation of the membranæ deciduæ.

According to Reichert, the ovum is completely enclosed at the twelfth or the thirteenth day. The mucous membrane lining the uterus becomes the decidua vera, and the border from which the new growth is formed which covers the ovum is the boundary between this and the decidua reflexa. The new growth, springing from this border, envelops the ovum completely, and is called the decidua reflexa; and, in this membrane, there is no trace of the uterine tubules.

As development advances, a portion of the decidua vera, the description of which we reserve for the present, under-

[1] REICHERT, *Beschreibung einer frühzeitigen menschlichen Frucht im bläschenförmigen Bildungszustande nebst vergleichenden Untersuchungen über die bläschenförmigen Früchte der Säugethiere und des Menschen.—Archiv für Anatomie, Physiologie und wissenschaftliche Medicin*, Leipzig, 1873, No. 1, S. 127, *et seq.* This article has also been published separately in 4o., with illustrations. (Idem, Berlin, 1873, S. 89.)

goes development into the maternal portion of the placenta. The rest of the decidua vera becomes extended, loses its vessels and glands, and is reduced to the condition of a simple membrane.

According tc Robin, the cylindrical epithelial cells of the mucous membrane of the body of the uterus, soon after fecundation, become gradually exfoliated, and their place is supplied by flattened epithelial scales, of the pavement-variety. This change is effected at from the sixth to the eighth week, and the pavement-cells are then found covering both the decidua vera and the reflexa. The epithelium of the cervix retains its cylindrical character, but most of the cells lose their cilia.[1]

During the first periods of utero-gestation, the two layers of decidua are separated by a small amount of an albuminous and sometimes a sanguinolent fluid; but this disappears at about the end of the fourth month, and the membranes then come in contact with each other.[2] They soon become so closely adherent as to form a single membrane, which is in contact with the chorion. Sometimes, at full term, the membranes of the fœtus can be separated from the decidua; but frequently all of the different layers are closely adherent to each other.

The changes we have just described are not participated in by the mucous membrane of the neck of the uterus. The glands in this situation secrete a semisolid, transparent, viscid mucus, which closes the os, and is sometimes called the uterine plug.

Toward the fourth month, a very delicate, soft, homogeneous layer appears over the muscular fibres of the uterus, beneath the decidua vera, which is the beginning of a new mucous membrane. This is developed very gradually, and

[1] ROBIN, *Mémoire sur quelques points de l'anatomie et de la physiologie de la muqueuse et de l'epithélium utérins pendant la grossesse.—Journal de la physiologie*, Paris, 1858, tome i., pp. 60, 61.

[2] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 868.

the membrane is completely restored about two months after parturition.

Such are the changes in the mucous membrane of the uterus which result in the formation of the membranæ deciduæ. We shall not discuss the old ideas of the formation of a decidua by an exudation from the mucous membrane, or the view that the mucous membrane extends over the openings of the Fallopian tubes, and that a portion of it is pushed into the uterus by the descending ovum to form the decidua reflexa, as these considerations have now only an historical interest. The mode of development of the decidua reflexa by a growth of the mucous membrane of the uterus over the ovum was discovered by Coste;[1] and this view has been but little modified by the observations of Reichert, which we have quoted so fully.

Development and Structure of the Placenta.—In describing the formation of the membranæ deciduæ and of the chorion, we have necessarily hinted at the mode of development of the placenta. Although there is considerable difference of opinion among anatomists with regard to the exact relations between the vessels of the mother and of the fœtus *in utero*, it is admitted by all that the fœtus derives its nourishment from the maternal blood, and that the placenta is, in addition, a respiratory organ. Reasoning from what we should consider to be the requirements of the fœtus, it would be natural to suppose that the fœtal vessels are bathed in maternal blood; and it is certain that the two sets of vessels have no direct communication with each other. It is also well known that the fœtus has an independent circulation, its heart beating about twice as fast as the heart of the mother. In our description of the placenta, we shall first give the views which we conceive to be correct, and then advance the facts and arguments by which these views are apparently supported.

[1] COSTE, *Développement des corps organisés*, Paris, 1849, Explanations of Plates ii., ii^a., vii., *espèce humaine.*

Beginning with the first development of the placenta, the observation which we have quoted from Reichert, in which, it will be remembered, the tufts of the fœtal chorion were actually drawn out of the tubules of the uterine mucous membrane, seems to demonstrate beyond question the fact of penetration of the villi of the chorion into the maternal tubes. This is a capital point in our view of the mode of development of the placenta; and this cannot be questioned, if we admit the accuracy of Reichert's description. It is certain that the portion of the chorion which eventually becomes attached to the uterus undergoes a much greater degree of development than the rest of the membrane. The villi in this situation become branched and arborescent; they are filled with blood-vessels, while the vascularity in other parts of the chorion disappears; the mucous membrane corresponding to this portion of the chorion also becomes thickened; the tubes in which the villi have penetrated are correspondingly enlarged and branched, and the vessels which surround them are increased in size; finally, the union between the villi and the tubes becomes so close that they cannot be separated from each other. It is evident that, if this be the mode of development of the placenta, the maternal portion is formed from a restricted and an hypertrophied part of the mucous membrane of the uterus, and the fœtal portion is simply an exceedingly vascular and villous part of the chorion.

As development advances, the vessels of the maternal portion of the placenta coalesce into great lakes, which communicate freely with the uterine sinuses. In these great cavities, we find the vascular fœtal tufts; and it is easy to understand how transudation of nutritive material and gases can take place from the blood of the mother to the vascular system of the fœtus.

If the above description be correct, we should be able to pass an injection from the uterine sinuses into the maternal portion of the placenta, even as far as its fœtal surface; but

this is a point concerning which there has been a great deal of discussion.

In injected specimens of the placenta, when an attempt has been made to fill the maternal as well as the fœtal vessels, the material injected into the uterine vessels has sometimes passed through the entire thickness of the placenta and appeared just beneath the transparent chorion at the fœtal surface of the organ. This appearance, however, has been thought by some writers to be due to extravasation; and many physiologists are of the opinion that the placenta has no maternal portion, that it is entirely a fœtal organ, and that the maternal vessels do not pass beyond the surface by which it is attached to the walls of the uterus. This opinion we believe to be erroneous; and we quote in full the following observation made by John Hunter, who was the first to give a correct idea of the relations between the maternal and the fœtal vessels:[1]

"The late indefatigable Dr. McKenzie, about the month of May 1754, when assistant to Dr. Smellie, having procured the body of a pregnant woman, who died undelivered at the full term, had injected both the veins and arteries with peculiar success; the veins being filled with yellow, the arteries with red.

"Having opened the abdomen, and exposed the uterus, he made an incision into the fore part, quite through its substance, and came to what seemed to be an irregular mass of injected matter. The appearance being new, he proceeded no further, and greatly obliged me, by desiring my attendance to examine parts, in which the appearances were so uncommon. The examination was made in his presence, and in the presence of several other gentlemen, whose names I have now forgotten; but I have reason to believe that some are settled in this country, who I hope will have an opportunity of perusing this publication.

[1] John Hunter, *On the Structure of the Placenta.—Observations on certain Parts of the Animal Œconomy*, London, 1792, p. 163.

"I first raised, with great care, a part of the uterus from the irregular mass, and in doing this, observed regular pieces of wax passing obliquely between it and the uterus, which broke off, leaving part attached to that mass; and on attentively examining the portions towards the uterus, they plainly appeared to be a continuation of the veins passing from it to this substance, which proved to be the placenta.

"I likewise observed other vessels, about the size of a crow-quill, passing in the same manner, although not so obliquely; these also broke upon separating the placenta and uterus, leaving a small portion on the surface of the placenta; and on examination they were discovered to be continuations of the arteries of the uterus. My next step was to trace these vessels into the substance of what appeared placenta, which was first attempted in a vein; but that soon lost the regularity of a vessel, by terminating at once upon the surface of the placenta in a very fine spongy substance; the interstices of which were filled with the yellow injected matter. This termination being new, I repeated the same kind of examination on other veins, which always led to the same terminations, never entering the substance of the placenta in the form of a vessel. I then examined the arteries, tracing them in the same manner toward the placenta, and found that, having made a twist, or close spiral turn upon themselves, they were lost on its surface. On a more attentive view, I perceived that they terminated in the same way as the veins; for opposite to the mouth of the artery, the spongy substance of the placenta was readily distinguished with the red injection intermixed.

"Upon cutting into the placenta I discovered, in many places of its substance, yellow injection, in others red, and in many others these two colours mixed. The substance of the placenta, now filled with injection, had nothing of the vascular appearance, nor that of extravasation, but had a regularity in its form which showed it to be naturally of a cellular structure, fitted to be a reservoir for blood.

"I perceived likewise, that the red injection of the arteries, (which had been first injected) had passed out of the substance of the placenta into some of the veins leading from the placenta to the uterus, mixing itself with the yellow injection; and that the spongy chorion, called the decidua, by Dr. Hunter, was very vascular, its vessels going to and from the uterus, being filled with the different coloured injections."

We have quoted the above in full, for the reason that this observation seems to show that the uterine vessels communicate with great sinuses or lakes of blood in the placenta. This view was at first pretty generally adopted by anatomists; but some observers subsequently denied this arrangement, supposing that the uterine vessels terminated at the placenta without penetrating this organ. Adopting, however, the Hunterian view of the arrangement of the maternal vessels, Reid showed, by injections of the umbilical vessels, that the fœtal tufts of the placenta were supplied with blood from the umbilical arteries, which was returned to the fœtus by the umbilical vein.[1]

The important point in the determination of the connection of what may be termed the placental maternal sinuses with the vessels of the uterus can be settled by injection of the uterine vessels in cases in which the observation can be made while the placenta is still attached to the uterine walls. Dalton, since 1853, has examined the parts *in situ* in four cases of women who died undelivered at or near the full term of pregnancy, and adopted the ingenious expedient of filling the uterine vessels with air, by which the course of the injection could be directly observed. This operation is performed in the following manner: The uterus, with its contents, is removed from the body, is carefully opened, and the fœtus is taken out, after dividing the umbilical cord. The parts are then placed under water, the end of a blow-pipe is

[1] Reid, *On the Anatomical Relations of the Blood-vessels of the Mother to those of the Fœtus in the Human Species.—Physiological Anatomical and Pathological Researches*, Edinburgh, 1848, p. 316, *et seq.*

introduced into one of the divided vessels of the uterine walls, and air is forced in by gentle insufflation. By this process, the venous sinuses of the uterus itself are first filled, next, the deeper portions of the placenta, and finally, "the bubbles of air insinuate themselves everywhere between the fœtal tufts, and appear in the most superficial portions of the placenta, immediately underneath the transparent chorion. If the chorion be now divided at any point by an incision, passing merely through its own thickness, the air, which was confined beneath it in the placental sinuses, will escape, and rise in bubbles to the surface of the water. Such an experiment shows conclusively that the placental sinuses communicate freely with the uterine vessels, occupy the entire thickness of the placenta, and are equally extensive with the tufts of the fœtal chorion." Dalton farther states that the uterine vessels, as they penetrate the placenta, have an exceedingly oblique direction, and that their orifices may be easily overlooked, but can be seen by careful inspection.[1]

We have no doubt with regard to the accuracy of the observations of Dalton, and we conceive that they have settled the question of the existence of a true maternal portion of the placenta. In corroboration of this, in 1864, we examined the uterus, with the placenta attached, of a woman who died in the latter months of pregnancy, in the presence of the late Prof. G. T. Elliot and Prof. J. P. White, and forced air from the uterine sinuses throughout the entire thickness of the placenta, between the fœtal tufts. In view of these facts, concerning which there can be no doubt, it seems unnecessary to discuss the more or less theoretical views of writers who have not made injections of the uterus with the placenta attached. The observations of Dalton have since been confirmed by numerous anatomists, among the latest of whom we may mention Prof. Turner, Dr. J. Matthews Duncan, and M. Laure; so that we must consider the fact of an

[1] DALTON, *Anatomy of the Placenta.* From the *American Medical Monthly*, New York, July, 1858, pp. 12, 14.

intra-placental circulation of maternal blood as definitively established.[1]

Structure of the Fully-developed Placenta.—The placenta of the human subject presents certain differences in its structure at various periods of utero-gestation, most of which have been indicated in treating of its development. At about the end of the third month, the limits of the placenta become distinct, and the organ rapidly assumes the anatomical characters observed after it may be said to be fully developed. It then occupies about one-third of the uterine mucous membrane, and is generally rounded or ovoid in form, with a distinct border connected with the decidua and the chorion. It is from seven to nine inches in diameter, a little more than an inch in thickness at the point of penetration of the umbilical cord, slightly attenuated toward the border, and weighs from fifteen to thirty ounces. Its fœtal surface is covered with the smooth amniotic membrane, and its uterine surface, when detached, is rough, and divided into numerous irregular lobes or cotyledons, from half an inch to an inch and a half in diameter. Between these lobes, are membranes, called dissepiments, which penetrate into the substance of the organ, frequently as far as the fœtal surface.[2]

Upon the uterine surface, is a thin, soft membrane, sometimes called the decidua serotina. This is merely a portion of the mucous membrane of the uterus situated next the muscular walls, the greater part of it not being thrown off with the placenta. It is composed of amorphous matter, numerous granulations, and colossal cells with enlarged and multiple nuclei. If we scrape the uterine surface of a fresh placenta, these cells appear, on microscopical observation, very much

[1] TURNER, *Observations on the Structure of the Human Placenta.—Journal of Anatomy and Physiology*, Cambridge and London, 1873, vol. vii., p. 133.

LAURE, *Le placenta.—Revue scientifique*, Paris, 1873–'74, tomes xii., xiii., p. 786.

[2] FARRE, *Cyclopædia of Anatomy and Physiology*, London, 1859, vol. v., Supplement, p. 715, *et seq.*, Article, *Uterus and its Appendages.*

like the so-called cancer-cells. There has been and is now con siderable difference of opinion with regard to the formation of the decidua serotina. Some writers, who do not admit that the placenta has any true maternal portion, regard it as the portion of decidua imprisoned between the chorion and the muscular walls of the uterus;[1] but, if we adopt the view that the placenta is formed in part of the uterine mucous membrane, we must regard the serotina, so called, as simply the deeper portion of this membrane.

Adopting the view, as we have, that the villi of the chorion are bathed in the maternal blood in the substance of the placenta, and that these villi originally penetrate the uterine tubules, the theory lately advanced by Ercolani, that the placenta contains utricular glands which elaborate a fluid for fœtal nutrition, from a theoretical point of view at least, is not necessary to explain the nutritive functions of the placenta. There is no reason to believe that there is any such process of secretion in the placenta; and it is more consistent to assume that there is a simple transudation of nutritive material from the blood of the mother through the vessels of the fœtal tufts. This opinion is not opposed to the demonstration, by Ercolani, of utricular glands, developed either from the original uterine tubules or of new formation; it simply does not admit the function ascribed to these glands by Ercolani, which rests upon purely theoretical considerations.[2]

Blood-vessels of the Placenta.—The two arteries of the umbilical cord branch upon the fœtal surface of the placenta beneath the amnion, and finally penetrate the substance of the organ. The branches of the veins, which are about six-

[1] ROBIN, *Mémoire sur quelques points de l'anatomie et de la physiologie de la muqueuse et de l'epithélium utérins pendant la grossesse.—Journal de la physiologie*, Paris, 1858, tome i., p. 50.

[2] ERCOLANI, *Mémoire sur les glandes utriculaires de l'utérus et sur l'organe glandulaire de nouvelle formation.—Journal de l'anatomie*, Paris, 1868, tome v., p. 501, *et seq.*

teen in number, converge toward the cord, and unite to form the umbilical vein. Upon the uterine surface, are numerous oblique openings of the veins which return the maternal blood to the uterine sinuses. There are also numerous small spiral arteries, which pass into the substance of the organ to supply blood to the maternal portion. These are the "curling arteries," described by John Hunter.[1]

If we inject the umbilical arteries, the fluid is returned by the umbilical vein, having passed through the vascular tufts of the fœtal portion of the placenta. According to Farre, the small arteries and the veins of the villi at first communicate through a true capillary plexus; but, toward the end of pregnancy, the capillaries disappear, leaving loops of vessels, "simple, compound, wavy, or much contorted, and in parts varicose."[2]

According to the recent researches of Winkler, there are three kinds of fœtal villi: 1. Those which terminate just beneath the chorion, without penetrating the vascular lacunæ. 2. Longer villi, which hang free in the lacunæ. 3. Long, branching villi, which penetrate more deeply into the placenta, some extending as far as its uterine surface.[3] Winkler does not admit the existence of perivascular spaces in the fœtal tufts, which have been described by Reitz.[4]

The formation of the great vascular lakes of the maternal portion of the placenta has already been described.[5] These, according to Winkler, present numerous trabeculæ, which extend from the uterine to the fœtal surface; and, between these trabeculæ, are numerous exceedingly delicate transverse and

[1] HUNTER, *On the Structure of the Placenta.—Observations on Certain Parts of the Animal Œconomy*, London, 1792, p. 171.

[2] FARRE, *op. cit.—Cyclopædia of Anatomy and Physiology*, London, 1859, vol. v., Supplement, p. 718.

[3] WINKLER, *Zur Kentniss der menschlichen Placenta.—Archiv für Gynaekologie*, Berlin, 1872, Bd. iv., S. 249.

[4] WINKLER, *op. cit.*, S. 253.

REITZ, in STRICKER, *Manual of Human and Comparative Histology*, The New Sydenham Society, London, 1873, vol. iii., p. 496.

[5] See page 378.

oblique secondary trabecular processes.[1] The chorionic villi, according to the recent observations of Hennig,[2] contain blood-vessels, which we have already described, surrounded by a gelatinous, connective-tissue structure (*Schleimgewebe*), and are generally covered with a layer of nucleated cells of pavement-epithelium.

In parturition, the curling arteries and the veins on the uterine surface of the placenta are torn off, and the placenta then consists of the parts we have just described; the torn ends of these vessels attached to the uterus are closed by the contractions of the surrounding muscular fibres; and the blood which is discharged is mainly derived from the placenta itself. Thus the very contractions which expel the contents of the uterus close the vessels and prevent loss of blood by the mother.

[1] WINKLER, *Zur Kentniss der menschlichen Placenta.—Archiv für Gynaekologie*, Berlin, 1872, Bd. iv., S. 240.

[2] HENNIG, *Studien über den Bau der menschlichen Placenta*, Leipzig, 1872, S. 19.

CHAPTER XVI.

DEVELOPMENT OF THE EMBRYON — THE OSSEOUS, MUSCULAR, CUTANEOUS, AND NERVOUS SYSTEMS.

General view of the development of the embryon—Development of the cavities and layers of the trunk in the chick—External blastodermic membrane—Intermediate membrane, in two layers—Internal blastodermic membrane—Neural canal—Chorda dorsalis—Primitive aortæ—Vertebræ—Origin of the Wolffian bodies—Pleuro-peritoneal cavity—Development of the skeleton—Ossification of the skeleton—Development of the muscles—Development of the skin—Development of the nervous system—Development of the encephalon—Development of the organs of special sense—Cartilage of Meckel.

The product of generation retains the name of ovum until the form of the body begins to be apparent, when it is called the embryon. At the fourth month, about the time of quickening, it is called the fœtus, a name which it retains during the rest of intra-uterine life. The membranes which we have described in the preceding chapter are appendages developed for the purposes of protection and nutrition; and the embryon itself, in the mammalia, is developed from a restricted portion of the layers of cells resulting from the segmentation of the vitellus.

In the preceding chapter, we have described the formation of the blastodermic cells and the appearance of the groove which is subsequently developed into the neural canal. At this portion of the ovum, there is a thickening of the blastoderm, which then presents three layers, the middle layer, the thickest and most important, being developed from the opposite surfaces of the external and the internal layer.[1] We have to study, then, the changes which take place in

[1] See page 360.

three layers of cells, which we shall call the external, the intermediate, and the internal blastodermic membranes. The earliest stages of development have been studied almost exclusively in the chick, and the processes here observed cannot be assumed to represent exactly the mode of development of the human subject. For this reason, we feel justified in adopting the simplest division of layers, which is into three, and shall not attempt to follow the excessively minute descriptions of the early arrangement of cells, given by some recent observers.

A general idea of the development of certain of the important parts of the embryon will aid us in comprehending the more minute processes and the formation of special organs; and this we can give without reference to the various divisions of the blastodermic layers adopted by different writers. It makes very little difference, indeed, as regards our actual knowledge of development, whether we restrict the external blastodermic membrane to the development of the epidermis, or whether we assume that a portion of it forms the walls of the neural canal. In the latter case, we simply make a thicker external layer at the expense of a portion of the intermediate layer. It is the discussion of such minor points as this, which depend mainly upon observations made upon the chick, that we propose to avoid, in our endeavor to make the description of the first processes of development as simple as possible.

We may assume that the furrow for the spinal canal and its dilated superior portion, the head, have been closed over by the union of the dorsal, or medullary plates behind. At a later period, there has been a growth of the abdominal, or visceral plates, which finally close over the front of the embryon. Now, to adopt, with slight modifications, a simile given by Hermann,[1] we may imagine a young mammal, with a short, straight alimentary canal, taking no account, for the present, of its glandular appendages. We take the entire

[1] HERMANN, *Grundiss der Physiologie*, Berlin, 1870, S. 469.

body as a tube, the caliber of which is the alimentary canal, with walls formed of concentric layers. Counting these layers from within outward, we have first, the mucous membrane; next, the muscular coat of the intestine; then, the visceral serous membrane, the parietal serous membrane, the muscles of the trunk with the bones; and finally, the integument. All of these layers are developed, to a greater or less degree, simultaneously, from different layers of the blastodermic cells. With the view that we shall adopt, the external blastodermic membrane becomes the epidermis, and the internal blastodermic membrane, the epithelium of the alimentary canal. The intermediate membrane splits into two layers, the outer layer becoming attached to the external blastodermic membrane and forming the muscular layer of the trunk, while the inner layer is connected with the internal blastodermic membrane and contributes to the formation of the viscera. At a later period, the extremities are developed, as solid processes connected with the outer layer of the intermediate membrane, and covered by a prolongation of the external blastodermic membrane.

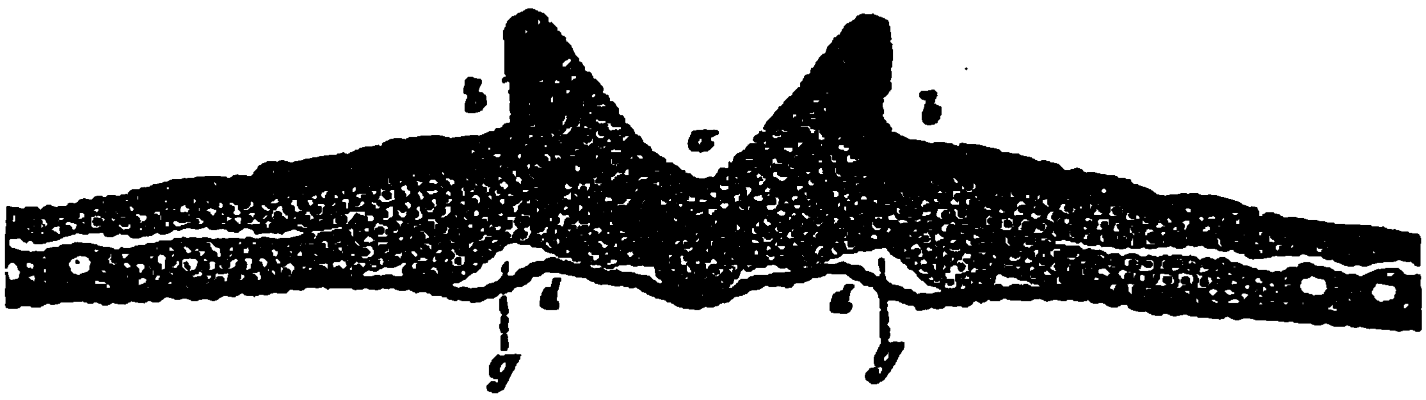
Development of the Cavities and Layers of the Trunk in the Chick.—As an introduction to a description of the development of special organs in the human subject and in mammals, it will be found very useful to study the first stages of development in the chick, by which we can get an idea of the arrangement of the different blastodermic layers, and the way in which they are developed into the different parts of the trunk, with the mode of formation of the great cavities. In doing this, we shall endeavor to describe the figures given by Brücke, which were photographed on wood from large diagrams, made from actual preparations, by Seboth.[1] In this description, we shall take no account of the formation of the membranes.

Fig. 37 illustrates one of the earliest stages of develop-

[1] BRÜCKE, *Vorlesungen über Physiologie*, Wien, 1873, Bd. ii., S. 276.

ment in the chick. In this figure, the superior layer of dark cells (*b*) represents the external blastodermic membrane. The inferior layer of dark cells (*d*) represents the internal blastodermic membrane. The middle layer of lighter cells is the intermediate membrane, which, toward the periphery, is split

FIG. 37.



into two layers. This figure represents a transverse section. At *a*, is a transverse section of the groove which is subsequently developed into the canal for the spinal cord. Beneath this groove, is a section of a rounded cord (*e*), the chorda dorsalis. The openings (*g*) represent the situation of the two aortæ. The other cavities are as yet indistinct in this figure.

FIG. 38.

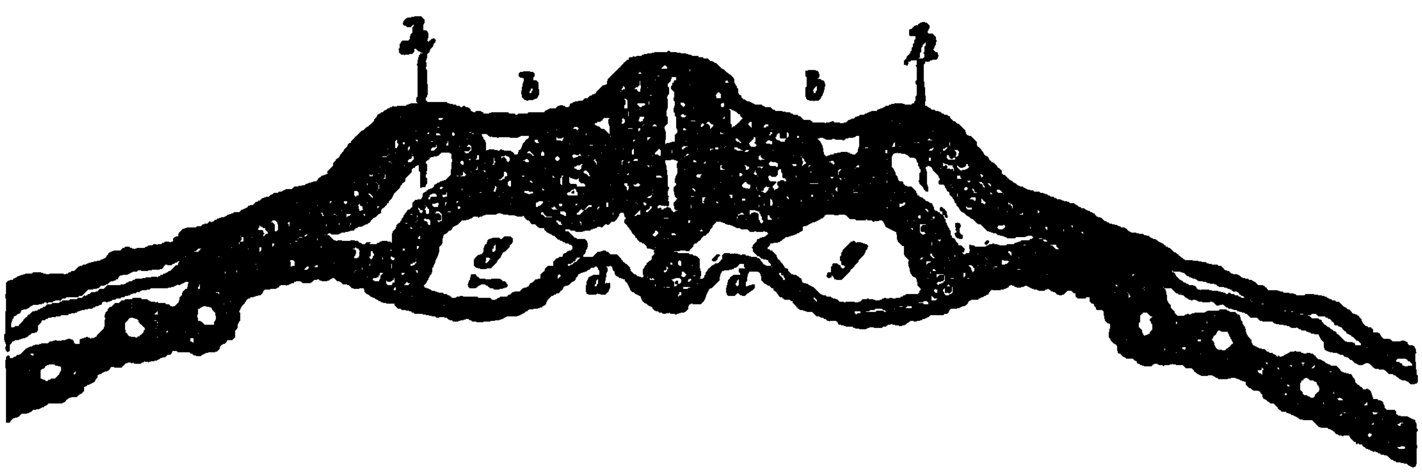


Fig. 38 shows the same structures at a more advanced stage of development. The dorsal, or vertebral plates which bound the furrow (*a*) in Fig. 37, are closed above, and include (*a*) the neural canal. The chorda dorsalis (*e*) is separated from the cells surrounding it in Fig. 37. We have still

the external blastodermic membrane (b) and the internal blastodermic membrane (d), presenting various curves which follow the arrangement of the cells of the intermediate layer. By the sides of the boundaries of the neural canal, are two distinct masses of cells (c), which are developed into the vertebræ. Outside of these masses of cells, are two smaller collections of cells, afterward developed into the Wolffian bodies, which will be described farther on. Beneath these two masses, are two large cavities (g), the largest cavities shown in Fig. 38, presenting an irregular form, which are sections of the two primitive aortæ. The two openings (h) become afterward the pleuro-peritoneal cavity.

FIG. 39.

In Fig. 39, the parts are still farther developed. The neural canal is represented (a) nearly the same as in Fig. 38, with the chorda dorsalis (e) just beneath it. A groove, or gutter (d) has been formed in front, which is the groove of the intestinal canal. This remains open at this time, and is lined by the internal blastodermic membrane. Just above d, is a single opening (g), which is formed by the union of the two openings (g) in Figs. 37 and 38, and this is the abdominal aorta, which has here become single. The two openings (h) represent a section of the pleuro-peritoneal cavity. The outer wall of this cavity is the outer visceral plate, which is developed into the muscular walls of the abdomen. The lower and inner wall is the inner visceral plate, which forms the main portion of the intestinal wall. The outer wall is the outer layer of the intermediate membrane, and the inner

wall is the inner layer of the same membrane. The two round orifices (*i*) are sections of the Wolffian ducts.[1]

The figures we have just described, it must be borne in mind, represent transverse sections of the body of the chick, made through the middle portion of the abdomen. In our explanations of these figures, we have not adhered absolutely to the text of Brücke, but have made use of the very elegant semi-diagrammatic illustrations by Waldeyer, whose explanations are remarkably clear and satisfactory.[2] Our explanations, however, particularly those of Fig. 39, are sufficiently extended to enable us to study the development of special organs. The posterior parts, it is seen, are developed first, the situation of the vertebral column being marked soon after the enclosure of the neural canal by the vertebral plates; and, at about the same time, the two aortæ make their appearance, with the first traces of the pleuro-peritoneal cavity. The next organs in the order of development, after the vascular system, are the Wolffian bodies, which are so large and important in the early life of the embryon. The intestinal canal is then a simple groove, and the embryon is entirely open in front. Were we now to follow the process of development farther, we should see that the visceral plates advance and close over the abdominal cavity, as the medullary plates have closed over the neural canal. Thus there would be formed a closed tube, the intestine, lined by the thin, internal blasto-

[1] A careful study of the process of development in the chick, as described by Reichert, an account which is still followed by some recent writers of authority (LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 880, *et seq.*), shows that the division of the blastodermic layers which we have adopted, as the one most nearly in accordance with the latest and most reliable observations, differs very little, in its essential features, from that proposed by this eminent German embryologist. Reichert accurately described the intermediate membrane, from which the greatest part of the embryon is developed, and regarded what we have termed the external and the internal blastodermic layers as of comparatively little importance. (REICHERT, *Das Entwickelungsleben im Wirbelthier-Reich*, Berlin, 1840, S. 102, *et seq.*)

[2] WALDEYER, *Eierstock und Ei*, Leipzig, 1870, Taf. iv.

dermic membrane, the walls of the intestine being formed of the inner layer of the intermediate membrane. This would bring the external layer of the intermediate membrane around the intestine to form the muscular walls of the abdomen, the cavity (Fig. 39, *h*) being the peritoneal cavity, and the external covering being the external blastodermic membrane. At this time, the great Wolffian bodies lie next the spinal column, between the intestine and the abdominal walls, with the single abdominal aorta situated behind the intestine.

Development of the Skeleton, Muscular System, and Skin.

Chorda Dorsalis.—One of the earliest structures observed in the developing embryon is the chorda dorsalis. This is situated beneath the neural canal, and extends the entire length of the body. It is formed of a cord of simple cells, and marks the situation of the vertebral column, though itself it is not developed into the vertebræ, which grow around it and encroach upon its substance, until it finally disappears. This structure has been very minutely described by Robin, under the name of the notocorde. According to Robin, in many mammals, the notocorde presents a slight enlargement at the cephalic extremity; which extends to the auditory vesicles, and it is somewhat diminished in size at the caudal extremity.[1] By the sides of this cord, are the masses of cells which are eventually developed into the vertebræ. The vertebræ, as they are developed, are formed of temporary cartilaginous structure, gradually extending around the chorda dorsalis, which then occupies the axis of the spinal column. Between the bodies of the vertebræ, the chorda dorsalis presents regular enlargements, surrounded by a delicate membrane. As ossification of the spinal column advances, that portion of the chorda dorsalis which is surrounded by the bodies of the vertebræ disappears, leaving the enlargements between the vertebræ distinct. These enlargements, which are not perma-

[1] ROBIN, *Mémoire sur l'évolution de la notocorde*, Paris, 1868, p. 8.

nent, are gradually invaded by fibrous tissue, their gelatinous contents disappear, and the intervertebral disks, composed of fibro-cartilaginous structure, remain. These disks are permanent between the cervical, the dorsal, and the lumbar ver-

FIG. 60.

The first six cervical vertebræ of the embryon of a rabbit, one inch in length.—*a b*, cephalic portion of the notocorde exposed by the removal of the cartilage; *b*, portion of the chorda dorsalis slightly enlarged, which, in this embryon, was situated between the atlas and the occipital bone; *c*, odontoid process; *d*, base of the odontoid process; *e*, inferior, or second part of the body of the axis; *f*, *k*, enlargements of the chorda dorsalis between the vertebræ; *g*, cartilage of the lateral portion of the atlas; *h*, lateral portion of the axis; *i*, *i*, transverse apophyses of the vertebræ. (LITTRÉ ET ROBIN, *Dictionnaire de médecine*, Paris, 1878, p. 1041.)

tebræ; but they eventually disappear from between the different parts of the sacrum and coccyx, as these are consolidated, this occurring, in the human subject, at from the ninth

to the twelfth year.[1] The processes of development just described are represented in Fig. 40.

Vertebral Column, Etc.—In Fig. 38 and 39 (*o*), are seen the two masses of cells, situated by the sides of the neural canal, which are destined to be developed into the vertebræ. These cells extend around and encroach upon the chorda dorsalis, and form the bodies of the vertebræ. They also extend over the neural canal, closing above, and these processes are called the medullary, or dorsal plates. Sometimes the dorsal plates fail to close at a certain point in the spinal column, and this constitutes the malformation known as spina bifida. From the sides of the bodies of the vertebræ, the various processes of these bones are formed. As the spinal column is developed, its lower portion presents a projection beyond the pelvis, which constitutes a temporary caudal appendage, curved toward the abdomen; but this no longer projects after the bones of the pelvis are fully developed. At the same time, the entire vertebral column is curved toward the abdomen, and it is twisted upon its axis from left to right, so that the anterior face of the pelvis presents a right angle to the upper part of the body; but, as the inferior extremities and the pelvis become developed, the spine becomes straight. The vertebræ make their appearance first in the middle of the dorsal region, from which point, they rapidly extend upward and downward, until the spinal column is complete.

FIG. 41.

Human embryo, about one month old, showing the large size of the head and upper parts of the body, the twisted form of the spinal column, the rudimentary condition of the upper and lower extremities, and the rudimentary tail at the end of the spinal column. (DALTON, *Human Physiology*, Philadelphia, 1871, p. 666.)

At the base of the skull, on either side of the superior

[1] ROBIN, *Mémoire sur l'évolution de la notocorde*, Paris, 1868, p. 10.

prolongation of the chorda dorsalis, are two cartilaginous processes, which are developed into the so-called cranial vertebræ. In this cartilaginous mass, three ossific points appear, one behind the other. The posterior point of ossification is for the basilar portion of the occipital bone, which is developed in the same way as one of the vertebræ; the middle point is for the posterior portion of the sphenoid; and the anterior point is for the anterior portion of the sphenoid. The frontal bone, the parietal bone, the temporal bone, and a portion of the occipital bone are developed from the connective tissue, without the intervention of preëxisting cartilaginous structure. The development of the face will be described separately. At the time when the vertebræ are being developed, with their laminæ and their spinous and transverse processes, the ribs extend over the thorax, and the clavicle, scapula, and sternum make their appearance.

At about the beginning of the second month, four papillary prominences, which are the first traces of the arms and legs, appear on the body of the embryon. These progressively increase in length, the arms appearing near the middle of the embryon, and the legs, at the lower portion. Each extremity is divided into three portions, the arm, forearm, and hand, for the upper extremities, and the thigh, leg, and foot, for the lower extremities. At the end of each extremity, there are, finally, divisions into the fingers and toes, with the various cartilages and bones of all of these parts, and their articulations.

Very early in intra-uterine life, the skeleton, which is at first entirely cartilaginous, begins to ossify, from little bony points which appear in the cartilaginous structure. The first points appear at nearly the same time (about the beginning of the second month) in the clavicle and the upper and the lower jaw. Similar ossific points, which gradually extend, are also seen in other parts, the head, ribs, pelvis, scapula, metacarpus and metatarsus, and the phalanges of the fingers and toes. At

birth, the carpus is entirely cartilaginous and does not begin to ossify until the second year; and the same is true of the tarsus, except the calcaneum and astragalus, which ossify just before birth. The pisiform bone of the carpus is the last to take on osseous transformation, this occurring at from the twelfth to the fifteenth year.[1] As ossification progresses, the deposits in the various ossific points gradually extend until they reach the joints, which remain incrusted with the permanent articular cartilage.

While the skeleton is being thus developed, the muscles are formed from the outer layer of the intermediate blastodermic membrane, and the visceral plates close over the thorax and abdomen in front, leaving an opening for the umbilical cord. According to Burdach, the various tissues of the external parts, particularly the muscles, begin to be distinct at the end of the second month.[2] The deep layers of the dorsal muscles are the first to be distinguished; then, successively, the long muscles of the neck, the anterior straight muscles of the head, the straight and transverse muscles of the abdomen, the muscles of the extremities, the superficial muscles of the back, the oblique muscles of the abdomen, and the muscles of the face.

The skin appears at about the beginning of the second month, when it is very delicate and transparent. At the end of the second month, the epidermis may be distinguished. The sebaceous follicles are developed at the third month; and, at about the fifth month, the surface is covered with their secretion mixed with desquamated epithelium. This cheesy substance constitutes the vernix caseosa.[3] At the third month, the nails make their appearance, and the hairs begin to grow at about the fifth month.[4] The sudoriparous glands first appear at about the fifth month, by the formation of flask-like processes of the true skin, which are gradually

[1] DALTON, *Human Physiology*, Philadelphia, 1871, p. 662.

[2] BURDACH, *Traité de physiologie*, Paris, 1838, tome iii., p. 416.

[3] See vol. iii., Secretion, p. 67. [4] BURDACH, *op. cit.*, p. 404, *et seq.*

elongated and convoluted, until they are fully developed only a short time before birth.[1]

Development of the Nervous System.

We have seen, in studying the development of the spinal column, how the dorsal, or medullary plates close over the groove for the neural canal. In the interior of this canal, the cerebro-spinal axis is developed, by cells, which gradually encroach upon its caliber, until we have remaining only the small central canal of the spinal cord, communicating with the ventricles of the brain. As the nervous tissue is developed in the interior of this canal, there is a separation of the histological elements at the surface, to form the membranes. The dura mater and the pia mater are formed first, appearing at about the end of the second month, while the arachnoid is not distinct until the fifth month.[2] The nerves, according to Longet, are not produced as prolongations from the cord into the various tissues, nor do they extend from the tissues to the cord; but they are developed, in each tissue, by a separation of histological elements from the cells of which the parts are originally constituted, which at first appear to be identical in their morphological characters.[3] The nerves of the sympathetic system are developed in the same way.

The mode of development of the spinal cord is thus sufficiently simple; but, with the growth of the embryon, we observe dilatations at the superior and at the inferior extremities of the neural canal. The cord is uniform in size in the dorsal region, marked only by the regular enlargements at the sites of origin of the spinal nerves; but we soon observe an ovoid dilatation below, which forms the lumbar enlargement, from which the nerves are given off to the inferior ex-

[1] BIESIADECKI, in STRICKER, *Manual of Human and Comparative Histology*, The New Sydenham Society, London, 1872, vol. ii., p. 240.

[2] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 898.

[3] *Loc. cit.*

tremities, and the brachial enlargement above, where the nerves of the superior extremities take their origin. At the same time, there is a more marked dilatation of the canal at its cephalic extremity. Here, a single enlargement appears, which is soon divided into three vesicles, called the anterior, middle, and posterior cerebral vesicles. These become more and more distinct as development advances. The formation of these parts is illustrated in Fig. 42, taken from Wagner, and made more distinct by Longet, as they are drawn upon a

FIG. 42.

A B C

Development of the nervous system of the chick.—A, the two primitive halves of the nervous system, twenty-four hours after incubation; B, the same, thirty-six hours after; C, the same, at a more advanced stage. c, the two primitive halves of the vertebræ; d, anterior dilatation of the neural canal; b, posterior dilatation (the lumbar enlargement); 1, 2, 3, anterior, middle, and inferior cerebral vesicles; a, slight flattening of the anterior cerebral vesicle; o, formation of the ocular vesicles. (LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 889.)

black ground. This figure, in C, shows the projections, on either side, of the vesicles which are eventually developed into the nervous portions of the organ of vision.

The three cerebral vesicles now undergo farther changes. The superior, which we may call the first primitive vesicle, enumerating them from above downward, is soon divided into two secondary vesicles, the anterior of which becomes the cerebral hemispheres, and the posterior, the optic thalami, which are eventually covered, by the greater relative develop-

ment of the hemispheres. The middle, or second primitive vesicle, does not undergo division, and is developed into the tubercula quadrigemina, or centres of vision. The posterior, or third primitive vesicle, is divided into two secondary vesicles, the anterior of which becomes the cerebellum, and the posterior, which is covered by the anterior, the medulla oblongata and the pons Varolii. While this division of the primitive cerebral vesicles is going on, the entire chain of encephalic ganglia becomes curved from behind forward,

FIG. 43.

Development of the spinal cord and brain of the human subject.
A, brain and spinal cord of an embryon of seven weeks, lateral view.
B, the same from an embryon farther advanced in development: *b*, spinal cord; *d*, enlargement of the spinal cord with its anterior curvature; *c*, cerebellum; *e*, tubercula quadrigemina; *f*, optic thalamus; *g*, cerebral hemispheres.
C, brain and spinal cord of an embryon of eleven weeks; *b*, spinal cord; *d*, enlargement of the spinal cord, with its anterior curvature; *c*, cerebellum; *e*, tubercula quadrigemina; *g*, cerebral hemispheres; *o*, optic nerve of the left side.
C′, the same parts in a vertical section in the median line from before backward; *b*, membrane of the spinal cord turned backward; *d*, second curvature of the upper portion of the spinal cord, which has become thickened and constitutes the peduncles of the cerebrum; *e*, tubercula quadrigemina; *f*, optic thalami covered by the hemispheres. (LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 892.)

forming three prominent angles. The first of these angles or prominences (*e*, Fig. 43, A, B, C), counting from before backward, is formed by a projection of the tubercula quadrigemina, which, at this time, constitute the most projecting portion of the encephalic mass; the second prominence (*c*, Fig. 43), situated behind the tubercula quadrigemina, is formed by the projection of the cerebellum; the third (*d*, Fig. 43, A, B, C), is the bend of the superior portion of the spinal cord. These projections and the early formation of certain parts of the encephalon in the human subject are illustrated in Fig. 43, taken from Tiedemann by Longet.

The cerebrum, as we have just seen, is developed from the anterior division of the first primitive cerebral vesicle. The development of this part is more rapid in its lateral portions than in the median line, which divides the cerebrum imperfectly into two lateral halves, forming, in this way, the great longitudinal fissure. At the same time, by the rapid development of the posterior portion, it extends over the optic thalami, the corpora quadrigemina, and the cerebellum. Up to the end of the fourth month, the hemispheres are smooth on their surface; but they then begin to present large depressions, following folds of the pia mater, which are the first convolutions, these increasing rapidly in number and complexity, especially after the seventh month.[1] The septum lucidum is then formed by an elevation of nervous matter from the base, which divides the lower portion of the space left between the hemispheres as they ascend, and forms the two lateral ventricles. At the base of these, are developed the corpora striata. The septum lucidum is formed of two laminæ, with a small space between them, which is the cavity of the fifth ventricle. The posterior division of this first primitive vesicle forms the optic thalami. These become separated in front into two lateral halves, but they remain connected together at their posterior portion, which becomes the posterior commissure. The central canal of the cord is prolonged upward between the optic thalami, and forms the third ventricle, which is covered by the hemispheres.

The second, or middle cerebral vesicle becomes filled with medullary substance, extends upward, and forms the peduncles of the cerebrum, the upper portion being divided to form the tubercula quadrigemina.

The anterior portion of the third primitive vesicle is developed into the cerebellum, the convolutions of which appear at about the fifth month. Its posterior portion forms the medulla oblongata, in the substance of which is the fourth ventricle, communicating with the third ventricle by a little

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 891.

canal, the aqueduct of Sylvius, which is left in the development of the middle vesicle. At about the fourth month, there is a deposition of nervous matter in front and above, forming the pons Varolii.[1]

In Fig. 42 (*C*, *o*), it is seen that the vesicles for the organs of vision appear very early, as lateral offshoots of the anterior cerebral vesicle. These gradually increase in size and advance anteriorly, as development of the other parts progresses. We shall see, when we come to study the development of the face, that the eyes are situated at first at the sides of the head, gradually approaching the anterior portion. At the extremity of each of these lateral prolongations, a rounded mass appears, which becomes the globe of the eye. The superficial portions of the globe are developed into the sclerotic and the cornea, which seem to be formed of a process from the dura mater. The pedicle attached to the globe becomes the optic nerve. The iris is developed at about the seventh week, and is at first a simple membrane, without any central opening. As the pupil appears, it is closed by a vascular membrane, which probably belongs to the capsule of the crystalline lens, and is called the pupillary membrane. This membrane gradually disappears by an atrophy extending from the centre to the periphery. It attains its maximum of development at the sixth month, and disappears at the seventh month. The vitreous humor is formed of the fluid contents of the optic vesicle. The crystalline lens is regarded as a product of the tegumentary layer. At the tenth week, we observe the beginning of the formation of the eyelids. These meet at about the fourth month and adhere together by their edges.[2] In many mammals, the eyelids remain closed for a few days after birth; but they become separated in the human subject in the later periods of fœtal life.

It is probable that the vesicle which becomes developed into the internal ear is formed independently; at least, cases

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 893

[2] Ibid., p. 896.

have been observed in which there was congenital absence of the auditory nerves, the parts of the internal ear being perfect. Soon after the formation of the auditory vesicle, however, it communicates with the third primitive cerebral vesicle, the filament of communication being developed into the auditory nerve.

The auditory vesicle, which appears subsequently to the organ of vision, is eventually developed into the vestibule. The next formations are the arches, or diverticula, which constitute the semicircular canals. According to Meckel, the membranous labyrinth appears long before the osseous labyrinth; and he has found it perfectly developed at three months.[1] The bones of the middle ear, which have no connection, in their development, with the nervous system, but which it is convenient to mention here, are remarkable for their early appearance. According to Meckel, who has described their development very accurately, they appear at the beginning of the third month, and are as large in the fœtus at term as in the adult. A remarkable anatomical point with relation to these structures is the existence of a cartilage, attached to the malleus on each side and extending from this bone along the inner surface of the lower jaw, the two cartilages meeting and uniting in the median line to form a single cord. "This cartilage now ossifies, although, in the commencement, it forms most of the mass of the bone; it disappears at the eighth month."[2] This curious structure has been very elaborately described by Robin and Magitot, and is known as the cartilage of Meckel.[3]

There are no special points for description in the development of the olfactory lobes, which is very simple. These are offshoots from the first cerebral vesicle, appearing at the inferior and anterior part of the cerebral hemispheres, a little

[1] MECKEL, *Manual of General, Descriptive, and Pathological Anatomy*, Philadelphia, 1832, vol. iii., p. 137.

[2] MECKEL, *loc. cit.*

[3] ROBIN ET MAGITOT, *Mémoire sur la genèse et le développement des follicules dentaires.—Journal de la physiologie*, Paris, 1860, tome iii., p. 15, *et seq.*

later than the parts connected with vision and audition. The vesicles themselves become filled with ganglionic matter, and constitute the olfactory bulbs, their pedicles being the so-called olfactory nerves, or commissures.

As far as the functions of the nervous system of the fœtus are concerned, it is probable that they are mainly restricted to reflex phenomena depending upon the action of the spinal cord, and that perception and volition hardly exist. It is probable that many reflex movements take place *in utero*. When a fœtus is removed from the uterus of an animal, even during the early periods of pregnancy, movements of respiration occur, a fact which we have often demonstrated to medical classes; and it is well known that efforts of respiration sometimes occur within the uterus. This we believe to be a reflex action excited by the want of oxygen in the tissues, when the placental circulation is interrupted. We have already discussed these phenomena in another volume.[1]

[1] See vol. i., Respiration, p. 487.

CHAPTER XVII.

DEVELOPMENT OF THE ALIMENTARY SYSTEM, THE RESPIRATORY SYSTEM, AND THE FACE.

First appearance of the intestinal canal—Formation of the mesentery—Formation of the stomach—Development of the large intestine—Appearance of the intestinal villi—Formation of the pharynx and œsophagus—Development of the anus—The liver, pancreas, and spleen—Development of the respiratory system—Development of the face—Visceral arches, and their development—Malformations of the face—Development of the teeth.

THE intestinal canal is the first formation of the alimentary system. As we have seen in Chapter XVI., this is at first open in the greatest part of its extent, presenting, at either extremity of the longitudinal gutter, in front of the spinal column, a rounded, blind extremity, which is closed over in front for a short distance. The closure of the abdominal plates then extends laterally and from the two extremities of the intestine, until we have only the opening remaining for the passage of the umbilical cord and the pedicle of the umbilical vesicle. There is at first an open communication between the lower part of the intestinal tube and the allantois, which forms the canal known as the urachus; but that portion of this communication which remains enclosed in the abdominal cavity becomes separated from the urachus, is dilated, and eventually forms the urinary bladder. When the bladder is first shut off, it communicates with the lower portion of the intestine, which is called the cloaca; but it finally loses this connection, and presents a special opening, the urethra.

As development advances, the intestine grows rapidly in

length and becomes convoluted. It is held loosely to the spinal column by the mesentery, a fold of the peritoneum, this membrane being reflected along the walls of the abdominal cavity. In the early stages of development, a portion of the intestine protrudes at the umbilicus, where the first intestinal convolution appears; and sometimes there is a congenital hernia of this kind at birth, which usually disappears under the influence of gentle and continued pressure. An illustration of this is given in Fig. 44. This protrusion, in the normal process of development, is gradually returned to the abdomen, as the cavity of the pedicle of the umbilical vesicle is obliterated, at about the tenth week.

FIG. 44.

Fœtal pig, showing a loop of intestine, forming an umbilical hernia; from a specimen in the possession of Prof. Dalton. From the convexity of the loop, a thin filament is seen passing to the umbilical vesicle, which is here flattened into a leaf-like form. (DALTON, *Human Physiology*, Philadelphia, 1871, p. 666.)

At the upper part of the abdominal cavity, the alimentary canal presents two lateral projections, or pouches. The one on the left side, as it increases in size, becomes the greater pouch of the stomach; and the one on the right side, the lesser pouch.

At a short distance below the attachment of the pedicle of the umbilical vesicle to the intestine, there appears a rounded diverticulum, which is eventually developed into the cæcum, or the commencement of the larger intestine. The cæcum gradually recedes from the neighborhood of the umbilicus, which is its original situation, and finally becomes fixed, by a shortening of the mesentery, in the right iliac region. As the cæcum, or caput coli, is developed, it presents a conical appendage, which is at first fully as large as the small intestine, and is relatively longer than in the adult. During the fourth week, this appendage becomes smaller and more or less twisted, forming the appendix vermiformis. At the second month, the

cæcum, or caput coli, as we have seen, is at the umbilicus, and the large intestine extends in a straight line toward the anus; at the third month, it is situated at about the middle of the abdomen; and it gradually descends, until it reaches the right iliac region at about the seventh month. Thus, at the second month, there is only a descending colon; the transverse colon is formed at the third month; and the ascending colon, at the fifth month. The ileo-cæcal valve appears at the third month; the rectum, at the fourth month; and the sigmoid flexure of the colon, at the fifth month.[1] During this time, the large intestine increases more rapidly in diameter than the small intestine, while the latter develops more rapidly in its length.

In the early stages of development, the surface of the intestines is smooth; but villi appear on its mucous membrane during the latter half of intra-uterine existence. These are found at first both in the large and the small intestine. At the fourth month, they become shorter and less numerous in the large intestine, and are lost at about the eighth month, when the projections which bound the sacculi of this portion of the intestinal canal make their appearance. The valvulæ conniventes appear, in the form of slightly-elevated, transverse folds, in the upper portion of the small intestine.[2] The villi of the small intestine are permanent.

The mesentery is first formed of two perpendicular folds, attached to the sides of the spinal column. As the intestine undergoes development, a portion of the peritoneal membrane extends in a quadruple fold from the stomach to the colon, to form the great omentum, which covers the small intestine in front.

As the head undergoes development, a large cavity appears, which is eventually bounded by the arches that are destined to form the different parts of the face. This is the pharynx. It is entirely independent, in its formation, of the intestinal canal, the latter terminating in a blind extremity at

[1] BURDACH, *Traité de physiologie*, Paris, 1838, tome iii., pp. 476, 477.

[2] Ibid, p. 470.

the stomach; and, between the pharynx and the stomach, there is at first no channel of communication. The anterior portion of the pharynx presents, during the sixth week, a large opening, which is afterward partially closed in the formation of the face. The rest of this cavity remains closed until a communication is effected with the œsophagus. The œsophagus appears in the form of a tube, which finally opens into the pharynx above and the stomach below. At this time, there is really no thoracic cavity, the upper part of the stomach is very near the pharynx, the œsophagus is short, the rudimentary lungs appear by its sides, and the heart lies just in front. As the thorax is developed, however, the œsophagus becomes longer, the lungs increase in size, and finally the diaphragm shuts off this cavity from the cavity of the abdomen. The growth of the diaphragm is from its periphery to the central portion, which gives passage to the vessels and the œsophagus. Sometimes, when this closure is incomplete, we have the malformation known as congenital diaphragmatic hernia.

The development of the anus is sufficiently simple. At first, as we have seen, the intestine terminates below in a blind extremity; but, at about the seventh week, a longitudinal slit appears below the external organs of generation, by which the rectum opens. This is the anus. It is not very unusual to observe an arrest in the development of this opening, the intestine terminating in a blind extremity, a short distance beneath the integument. This constitutes the malformation known as imperforate anus, a deformity which can usually be relieved, without much difficulty, by a surgical operation, if the distance between the rectum and the skin be not too great. The opening of the anus appears about a week after the opening of the mouth,[1] at or about the seventh week.

The rudiments of the liver appear very early, and, indeed, at the end of the first month, this organ has attained

[1] Burdach, *Traité de physiologie*, Paris, 1838, tome iii., pp. 467, 468.

an enormous size. According to Bischoff,[1] two projections, or buds, appear on either side of the intestine, which form the two principal lobes of the liver. This organ is at first symmetrical, the two lobes being of nearly the same size, with a median fissure. One of these prolongations from the intestine becomes perforated, and forms the excretory duct, of which the gall-bladder, with its duct, is an appendage. During the early part of fœtal life, the liver occupies the greatest part of the abdominal cavity. According to Burdach, its weight, in proportion to the weight of the body at different ages, is as follows: At the end of the first month, 1 to 3; at term, 1 to 18; in the adult, 1 to 36.[2] Its structure is very soft during the first months, and it is only at about the fourth or fifth month that it assumes one of its most important functions; viz., the production of sugar.[3] As development advances, and as the relative size of the liver gradually diminishes, its tissue becomes more solid.

The pancreas appears at the left side of the duodenum, by the formation of two ducts leading from the intestine, which branch and develop glandular structure at their extremities. The spleen is developed, about the same time, at the greater curvature of the stomach. This organ is abundantly supplied with blood-vessels, but has no excretory duct. According to Meckel, the spleen becomes distinct during the second month.[4]

There is no reason to believe that any of the digestive fluids are secreted during intra-uterine life. The stomach, at least, never contains, at this time, an acid secretion. At birth, the intestine contains a peculiar substance, called meconium, which will be described farther on. Cholesterine, an important constituent of the bile, is found in the meco-

[1] BISCHOFF, *Traité du développement de l'homme et des mammifères.—Encyclopédie anatomique*, Paris, 1843, tome viii., p. 330.

[2] BURDACH, *Traité de physiologie*, Paris, 1838, tome iii., p. 483.

[3] BERNARD, *Leçons sur la physiologie expérimentale*, Paris, 1855, p. 82.

[4] MECKEL, *Manual of General, Descriptive, and Pathological Anatomy*, Philadelphia, 1832, vol. iii., p. 321.

nium in large quantity, but its function is connected exclusively with excretion.[1]

Development of the Respiratory System.

On the anterior surface of the membranous tube which becomes the œsophagus, an elevation appears, which soon presents an opening into the œsophagus, the projection forming, at this time, a single, hollow *cul-de-sac.* This opening becomes the rima glottidis, and the single tube with which it is connected is developed into the trachea. At the lower extremity of this tube, a bifurcation appears, terminating first in one, and afterward, in several *culs-de-sac.* The bifurcated tube constitutes, after the lungs are developed, the primitive bronchi, at the extremities of which are the branches of the

FIG. 45.

Formation of the bronchial ramifications and of the pulmonary cells.—A, B, development of the lungs, after Rathke; C, D, histological development of the lungs, after J. Müller. (LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 907.)

bronchial tree. As the bronchi branch and subdivide, they extend downward into what becomes eventually the cavity of the thorax. The pulmonary vesicles, according to Burdach, are developed before the trachea. The lungs contain no air at any period of intra-uterine life, and receive but a small quantity of blood; but, at birth, they become distended with air, are increased thereby in volume, and receive all the blood from the right ventricle. This process of development is illustrated in Fig. 45. According to Burdach, the

[1] See vol. iii., Excretion, p. 267; *et seq.*

lungs appear, in the human embryon, during the sixth week. The two portions into which the original bud is bifurcated constitute the true pulmonary structure, and the formation of the trachea and bronchial tubes occurs afterward and is secondary.[1] We have indicated the pulmonary structure as branching processes from the bronchial tubes, merely for convenience of description.

Development of the Face.

The development of the face in the embryon of mammals is somewhat complex, but it is peculiarly interesting, as its study enables us to comprehend the manner in which various very common malformations of the face and palate are produced. The anterior portion of the embryon, as we have seen in studying the development of the trunk, remains open in front long after the medullary plates have met at the back and enclosed the neural canal. The common cavity of the thorax and abdomen is closed by the growth of the visceral plates, which meet in front. These are projecting plates of the intermediate blastodermic layer, which gradually extend forward from the vertebral column. At the same time that the visceral plates are thus closing over the thorax and abdomen, four distinct, tongue-like projections appear, one above the other, by the sides of the neck. These are called the visceral arches, and the slits between them are called the visceral clefts.[2] The first three arches, enumerating from above downward, correspond, in their origin, to the three primitive cerebral vesicles. The fourth arch, which is not enumerated by some authors, who recognize but three arches, corresponds to the superior cervical vertebræ. Of these four arches, the first is the most important, as its development, in connection with that of the frontal process, forms the face and the malleus and incus of the middle ear; the second arch

[1] BURDACH, *Traité de physiologie*, Paris, 1838, tome iii., pp. 484, 486.

[2] These arches correspond to the branchial vascular arches, which will be fully described in connection with the development of the circulatory system.

forms the lesser cornua of the hyoid bone, the stapes, and the styloid ligament; the third arch forms the body and the greater cornua of the hyoid; and the fourth arch forms the larynx. The first cleft, situated between the first and the second arch, becomes obliterated in front by a deposition of plastic matter, but an opening remains by the side, which forms, externally, the external auditory meatus, and internally, the tympanic cavity and the Eustachian tube. The other clefts become obliterated as the arches advance in their development.

From the above sketch, it is seen that the face and the neck are formed by the advance and closure in front of projections from behind, in the same way as the cavities of the thorax and abdomen are closed; but the closure of the first visceral arch is complicated by the projection, from above downward, of the frontal, or intermaxillary process, and by the formation of several secondary projections, which leave certain permanent openings, forming the mouth, nose, etc. These processes of development, we shall now attempt to follow.

In the very first stages of development of the head, there is no appearance of the face. The cephalic extremity consists simply of the cerebral vesicles, the surface of this enlarged portion of the embryon being covered, in front, as well as behind, by the external blastodermic membrane. During the sixth week, after the cavity of the pharynx has appeared, the membrane gives way in front, forming a large opening, which may be called the first opening of the mouth. At this time, however, the face is entirely open in front as far back as the ears. The first, or the superior visceral arch, now appears as a projection of the middle blastodermic layer, extending forward. This is soon marked by two secondary projections, the upper projection forming the superior maxillary portion of the face, and the lower, the inferior maxilla. The two projections which form the lower jaw soon meet in the median line, and their superior margin is the lower

lip. At the same time, there is a projection from above, extending between the two superior projections, which is called the frontal, or intermaxillary process. This extends from the forehead, that portion which covers the front of the cerebrum, downward. The superior maxillary projections then advance forward, gradually passing to meet the frontal process, but leaving two small openings on either side of the median line, which are the openings of the nostrils. The upper portion of the frontal process thus forms the nose; but below, is the lower end of this process, which is at first split in the median line, projects below the nose, and forms the incisor process, at the lower border of which are finally developed the incisor teeth. As the superior maxillary processes advance forward, the eyes are moved, as it were, from the sides of the head and present anteriorly, until finally their axes become parallel. These processes advance from the two sides, come to the sides of the incisor process beneath the nose, unite with the incisor process on either side, and their lower margin, with the lower margin of the incisor process, forms the upper lip; but, before this, the two lateral halves of the incisor process have united in the median line. At the bottom of the cavity of the mouth, a small papilla makes its appearance, which gradually elongates and forms the tongue.

While this process of development of the anterior portion of the first visceral arch is going on, at its posterior portion, we have developing, the malleus and incus, the former being at first connected with the cartilage of Meckel, which extends along the inner surface of the inferior maxilla, the two cartilages meeting at the chin. The cleft between the first and the second visceral arch has closed, except at its posterior portion, where an opening is left for the external auditory meatus, the cavity of the tympanum, and the Eustachian tube.

At the same time, the second visceral arch advances, and forms the stapes, the styloid ligament, and the lesser cornua

of the hyoid bone. The third arch advances in the same way; and the arches from the two sides meet, become united in the median line, and form the body and the greater cornua of the hyoid. The clefts between the second and third and between the third and fourth arches become obliterated by the deposition of plastic matter.

The fourth arch forms the sides of the neck and the larynx, the arytenoid cartilages being developed first. In front of the larynx and just behind the tongue, is a little elevation, which is developed into the epiglottis.

Fig. 46.

Mouth of a human embryon of from twenty-five to twenty-eight days; magnified fifteen diameters.—1, median or frontal process, the inferior portion of which is considerably enlarged; 2, right nostril; 3, left nostril; 4, 4, inferior maxillary processes, already united in the median line; 5, 5, superior maxillary processes, which have become quite prominent and have descended to the level of the slope of the frontal process; 6, mouth; 7, first visceral arch; 8, second visceral arch; 9, third visceral arch; 10, eye; 11, ear. (Sappey, *Traité d'anatomie*, Paris, 1874, tome iv., p. 72.)

According to Burdach, who has noted with great accuracy the time of development of different parts of the embryon, the openings of the nostrils appear in the second half of the second month; a little elevation, the nose, appears between these openings, and the nasal cavity begins to be separated from the mouth. The lips are distinct during the third month, and the tongue first appears in the course of the seventh week.[1]

The above sketch of the mode of development of the face enables us to understand the origin of certain of the more common malforma-

[1] Burdach, *Traité de physiologie*, Paris, 1838, tome iii., pp. 496, 498.

tions of this part. When, by an arrest of development, the superior maxilla on one side fails to unite with the side of the incisor process, we have the very common deformity known as single hare-lip. If this union fail on both sides, we have double hare-lip, when the incisor process is usually more or less projecting. As a very rare deformity, it is sometimes observed that the two sides of the incisor process

FIG. 47. FIG. 48.

10
3

Fig. 47.—Mouth of a human embryon of thirty-five days.—1, frontal process widely sloped at its inferior portion; 2, 2, incisor processes produced by this sloping; 3, 3, nostrils; 4, lower lip and maxilla, formed by the union of the inferior maxillary processes; 5, 5, superior maxillary processes contiguous to the incisor process; 6, mouth, still confounded with the nasal fossæ; 7, appearance of the closure of the nasal fossæ; 8, 8, appearance of the two halves of the palatine arch; 9, tongue; 10, 10, eyes; 11, 12, 13, visceral arches. (SAPPEY, *Traité d'anatomie*, Paris, 1874, tome iv., p. 78.)

Fig. 48.—Mouth of an embryon of forty days.—1, first appearance of the nose; 2, 2, first appearance of the alæ of the nose; 3, appearance of the closure beneath the nose; 4, middle, or median portion of the upper lip, formed by the approach and union of the two incisor processes, a little notch in the median line still indicating the primitive separation of the two processes; 5, 5, superior maxillary processes, forming the lateral portions of the upper lip; 6, 6, groove for the development of the lachrymal sac and the nasal canal; 7, lower lip; 8, mouth; 9, 9, the two lateral halves of the palatine arch, already nearly approximated to each other in front, but still widely separated behind. (SAPPEY, *Traité d'anatomie*, Paris, 1874, tome iv., p. 78.)[1]

[1] The periods of development indicated for these diagrams are somewhat earlier than those which we have quoted from Burdach; but it is impossible to fix these with absolute accuracy, and all the estimates given by authors are understood to be merely approximative.

have failed to unite with each other, leaving a fissure in the median line.

It is somewhat difficult to comprehend the exact mode of development of the face by verbal description alone; but it will be readily understood, after the account we have just given, by studying Figs. 46, 47, and 48, copied from the great atlas of Coste.

The palatine arch is developed by two processes, which arise on either side from the incisor process, pass backward and upward, and finally meet and unite in the median line. The union of these forms the plane of separation between the mouth and the nares; and want of fusion of these processes, from arrest of development, produces the malformation known as cleft palate, in which the fissure is always in the median line. At the same time, a vertical process forms in the median line, between the palatine arch and the roof of the nasal cavity, which separates the two nares.

Development of the Teeth.—Recent embryological researches, particularly those of Legros and Magitot, have shown that the old idea of the development of the dental papillæ in the bottom of a gutter formed at the border of either jaw is erroneous. According to these observers, whose descriptions seem to be exact and reliable, the first appearance of the organs for the development of the teeth is marked by the formation of a cellular projection extending the entire length of the rounded border of each jaw, which forms a rounded band above, and dips down somewhat into the subjacent structure. This band is readily separated by maceration, and the removal of the portion that dips into the maxilla leaves a groove, which is thought by Legros and Magitot to be the explanation of the description of a groove by the earlier writers.[1] This band extends the entire length of the jaws without interruption. Its superior surface is rounded, and that portion which dips into

[1] Legros et Magitot, *Contributions à l'étude du développement des dents.*—*Journal de l'anatomie*, Paris, 1873, tome ix., p. 455.

the subjacent mucous structure is wedge-shaped, so that its section has the form of a V.

As soon as this primitive band is formed, which occurs at the sixth or seventh week, a flat band projects from its internal surface, near the mucous structure, which Legros and Magitot call the epithelial band. This also extends over the entire length of the jaws. It is thin, flattened, with its free edge curved inward and toward the jaw, and is composed, at first, of a central layer of polygonal cells, covered by a layer of columnar epithelium.

At certain points, these points corresponding to the situations of the true dental bulbs, there appear rounded enlargements at the free margin of the epithelial band just described. Each one of these is developed into one of the structures of the perfect tooth. The mechanism of the formation of this, which is called the enamel-organ, and of the dental bulb is as follows:

A rounded enlargement appears at the margin of the epithelial band. This soon becomes directed downward (adapting our description to the lower jaw) and dips into the mucous structure, being at first connected with the epithelial band by a narrow pedicle, which soon disappears, leaving the enlargement enclosed completely in a follicle. This is the dental follicle, and has no connection with the wedge-shaped band which we described first. While this process is going on, a conical bulb appears at the bottom of the follicle. The enamel-organ, formed from the epithelial band, becomes excavated or cup-shaped at its under surface, and fits over the dental bulb, becoming united to it.

The tooth, at this time, consists of the dental bulb, with the enamel-organ closely fitted to its projecting surface. The enamel-organ is developed into the enamel; the dental bulb, which is provided with vessels and nerves, becomes the tooth-pulp; and, upon the surface of the dental bulb, the dentine, or ivory, is developed in successive layers. The cement is developed by successive layers upon that portion of

the dentine which forms the root of the tooth. As these processes go on, the tooth projects more and more, the upper part of the wall of the follicle gives way, and the tooth finally appears at the surface.

The permanent teeth are developed beneath the follicles of the temporary, or milk-teeth. The first appearance is a prolongation or diverticulum from the enamel-organ of the temporary tooth, which dips more deeply into the mucous structure. This becomes the enamel-organ of the permanent tooth; and the successive stages of development of the dental follicles and the dental pulp progress in the same way as in the temporary teeth. As the permanent teeth increase in size, they gradually encroach upon the roots of the temporary teeth. The roots of the latter are absorbed, the permanent teeth advance more and more toward the surface, and the crown of each temporary tooth is finally pushed out. The number of the temporary teeth is twenty, while there are thirty-two permanent teeth. Thus there are three permanent teeth on either side of both jaws, which are developed *de novo*, and are not preceded by temporary structures.[1]

The first dental follicles usually appear in regular succession. The follicles for the internal incisors of the lower jaw appear first, this occurring at about the ninth week. All of the follicles for the temporary teeth are completely formed at about the eleventh or the twelfth week.

The temporary teeth appear successively, the corresponding teeth appearing a little earlier in the lower jaw. The usual order, subject to certain exceptional variations, is as follows:

The four central incisors appear from six to eight months after birth.

The four lateral incisors appear from seven to twelve months after birth.

The four anterior molars appear from twelve to eighteen months after birth.

The four canines appear from sixteen to twenty-four months after birth.

The four posterior molars appear from twenty-four to thirty-six months after birth.

[1] For an account of the structure of the teeth, see vol. ii., Alimentation, p. 189, *et seq.*

The order of eruption of the permanent teeth is as follows:[1]

The two central incisors of the lower jaw appear from the sixth to the eighth year.

The two central incisors of the upper jaw appear from the seventh to the eighth year.

The four lateral incisors appear from the eighth to the ninth year.

The four first bicuspids appear from the ninth to the tenth year.

The four canines appear from the tenth to the eleventh year.

The four second bicuspids appear from the twelfth to the thirteenth year.

The above are the permanent teeth which replace the temporary teeth. The permanent teeth which are developed *de novo* appear as follows:

The first molars appear from the sixth to the seventh year.

The second molars appear from the twelfth to the thirteenth year.

The third molars appear from the seventeenth to the twenty-first year.

[1] SAPPEY, *Traité d'anatomie*, Paris, 1874, tome iv., pp. 113, 116, 119.

CHAPTER XVIII.

DEVELOPMENT OF THE GENITO-URINARY AND OF THE CIRCULATORY SYSTEM.

Development of the Wolffian bodies—Ducts of the Wolffian bodies and ducts of Müller—Development of the Wolffian ducts into the vasa deferentia, and of the ducts of Müller into the Fallopian tubes—Development of the testicles and ovaries—Development of the urinary apparatus—External organs of generation—Malformations of the external generative organs—Hermaphroditism—Development of the circulatory system—First, or vitelline circulation—Second, or placental circulation—Branchial arches and development of the arterial and the venous system—Development of the heart—Description of the fœtal circulation—Third, or adult circulation.

THE genital and the urinary organs are developed together, and are both preceded by the appearance of two large, symmetrical structures, known as the Wolffian bodies, or the bodies of Oken. These are sometimes called the false or the primordial kidneys. They appear at about the thirtieth day, develop very rapidly on either side of the spinal column, and are so large as to almost fill the cavity of the abdomen. Fig. 49, representing a specimen in the possession of Prof. Dalton, shows how large these bodies are in the early life of the embryon, at which time their function is undoubtedly very important.

Very soon after the Wolffian bodies have made their appearance, we can distinguish, at their inner borders, two ovoid bodies, which are finally developed into the testicles, for the male, or the ovaries, for the female. At their external borders, are two ducts, on either side, one of which, the internal, is called the duct of the Wolffian body. This finally disappears, in the female, but is developed into the vas deferens,

in the male. The other duct, which is external to the duct of the Wolffian body, disappears, in the male, but becomes the Fallopian tube, in the female.[1] This is known as the duct of Müller. Behind the Wolffian bodies, are developed the kidneys and the suprarenal capsules.

As the development of the Wolffian bodies attains its maximum, their structure becomes somewhat complex. From their proper ducts, which are applied directly to their outer borders, tubes make their appearance at right angles to the ducts, which extend into the substance of the bodies and become somewhat convoluted at their extremities. These tubes communicate directly with the ducts, and the ducts themselves open into the lower part of the intestinal canal, opposite to the point of its communication with the allantois. The tubes of the Wolffian bodies are simple, terminating in single, somewhat dilated, blind extremities, are lined with epithelium, and are penetrated, at their extremities, by blood-vessels, which

FIG. 40.

Fœtal pig, $\frac{5}{8}$ of an inch long; in the possession of Prof. Dalton.—1, heart; 2, anterior extremity; 3, posterior extremity; 4, Wolffian body. The abdominal walls have been cut away, in order to show the position of the Wolffian bodies. (DALTON, *Human Physiology*, Philadelphia, 1871, p. 675.)

[1] HENLE, *Handbuch der systematischen Anatomie des Menschen*, Braunschweig, 1866, Bd. ii., S. 342, 343; BRÜCKE, *Vorlesungen über Physiologie*, Wien, 1873, Bd. ii., S. 289.

The old idea was that the ducts of Müller become the vasa deferentia, and that the duct of the Wolffian bodies disappears, both in the male and in the female; but later researches show that the testicles become united to the Wolffian bodies, the remains of these bodies forming the head of the epididymis, and that the Wolffian ducts become the vasa deferentia. In the *Journal of Anatomy and Physiology*, Cambridge and London, 1868, vol. ii., p. 401, is an account of a case of true lateral hermaphroditism, observed by Dr. Rawdon, in which, in the left broad ligament, there was a Fallopian tube, but no ovary; while, in the right broad ligament, were found, an ovary with its Fallopian tube, and a testicle with an epididymis and a vas deferens. If this description be correct, it is a strong argument in favor of the view that the Fallopian tubes and the vasa deferentia are developed from distinct structures; the Fallopian tubes, from the ducts of Müller, and the vasa deferentia, from the ducts of the Wolffian bodies.

form coils or convolutions in their interior.[1] These are undoubtedly organs of depuration for the embryon, and take on the function to be subsequently assumed by the kidneys; but, in the female, they are temporary structures, disappearing as development advances, and having nothing to do with the development of the true urinary organs.

The testicles or ovaries are developed at the internal and anterior surface of the Wolffian bodies, first appearing in the form of small, ovoid masses. Beginning just above and passing along the external borders of the Wolffian bodies, are the tubes called the ducts of Müller. These at first open into the intestine, near the point of entrance of the Wolffian ducts. In the female, their upper extremities remain free, except the single fimbria which is connected with the ovary. Their inferior extremities unite with each other, and, at their point of union, form the uterus. When this union is incomplete, we have the malformation known as double uterus, which may be associated with a double vagina. We have referred to a case of this kind in a previous chapter.[2] The Wolffian bodies and their ducts disappear, in the female, according to Longet, at about the fiftieth day. A portion of their structure, however, persists, in the form of a collection of closed tubes, constituting the parovarium, or organ of Rosenmüller.[3]

In the female, the ovaries pass down no farther than the pelvic cavity; but the testicles, which are at first in the abdomen of the male, finally descend into the scrotum. As the testicles descend, they carry with them the Wolffian duct, that portion of the Wolffian body which is permanent constituting the head of the epididymis. At the same time, a cord appears, attached to the lower extremity of the testicle and extending to the symphysis pubis. This is called the gubernaculum testis. It is at first muscular, but the muscular fibres disappear during the later periods of utero-gesta-

[1] DALTON, *Human Physiology*, Philadelphia, 1871, p. 676.

[2] See page 347, note.

[3] See page 278.

tion. It is not known that its muscular structure takes any part, by contractile action, in the descent of the testicle in the human subject. The epididymis and the vas deferens are formed from the Wolffian body and the Wolffian duct.[1]

At about the end of the seventh month, the testicle has reached the internal abdominal ring;[2] and, at this time, a double tubular process of peritoneum, covered with a few fibres from the lower portion of the internal oblique muscle of the abdomen, gradually extends into the scrotum. The testicle descends, following this process of peritoneum, which latter becomes eventually the visceral and parietal portion of the tunica vaginalis. The canal of communication between the abdominal cavity and the cavity of the scrotum is finally closed, and the tunica vaginalis is separated from the peritoneum. The fibres derived from the internal oblique constitute the cremaster muscle.

At the eighth or the ninth month, the testicles have reached the external abdominal ring, and then soon descend into the scrotum.[3] The vas deferens, as we have seen, passes from the testicle, along the base of the bladder, to open into the prostatic portion of the urethra; and, as development advances, two sacculated diverticula from these tubes make their appearance, which are attached to the bladder and constitute the vesiculæ seminales.

As the ovaries descend to their permanent situation in the pelvic cavity, there appears, attached to the inner extremity of each, a rounded cord, analogous to the gubernaculum testis. A portion of this, connecting the ovary with the uterus, constitutes the ligament of the ovary; and the in-

[1] According to Henle, Brücke, and others, the ducts of the Wolffian bodies become the vasa deferentia, and the ducts of Müller, in the male, are temporary structures. This destroys the complete analogy which has been assumed to exist between the vasa deferentia and the Fallopian tubes. (HENLE, *Handbuch der systematischen Anatomie des Menschen*, Braunschweig, 1866, Bd. ii., S. 342, 343; BRÜCKE, *Vorlesungen über Physiologie*, Wien, 1873, Bd. ii., S. 289.)

[2] BURDACH, *Traité de physiologie*, Paris, 1838, tome iii., p. 590.

[3] Ibid.

ferior portion forms the round ligament of the uterus, which passes through the inguinal canal and is attached to the symphysis pubis.

The development of the external organs of generation will be studied after we have described the development of the urinary apparatus.

Development of the Urinary Apparatus.—Behind the Wolffian bodies, and developed entirely independently of them, the kidneys, suprarenal capsules, and ureters make their appearance. The kidneys are developed in the form of little, rounded bodies, composed of short, blind tubes, all converging toward a single point, which is the hilum. These tubes increase in length, branch, become convoluted in a certain portion of their extent, and finally assume the structure and arrangement of the renal tubules, with their Malpighian bodies, blood-vessels, etc. They all open into the hilum. At the same time that the kidneys are undergoing development, the suprarenal capsules are formed at their superior extremities. These bodies, the function of which is unknown, are relatively so much larger in the fœtus than in the adult, that they have been supposed to be peculiarly important in intra-uterine life, though nothing definite is known upon this point. The kidneys are relatively very large in the fœtus. According to Meckel, their proportion to the weight of the body, in the fœtus, is 1 to 80, and, in the adult, 1 to 240.[1] The ureters are undoubtedly developed as tubular processes from the kidneys, which finally extend to open into the bladder. This fact is shown by certain cases of malformation, in which the ureters have not reached the bladder, but terminate in blind extremities.[2] The development of the genito-urinary system can be readily understood, after the description we have just given, by a study of Fig. 50.

[1] MECKEL, *Manual of General, Descriptive, and Pathological Anatomy*, Philadelphia, 1832, vol. iii., p. 332.

[2] ISIDORE GEOFFROY SAINT-HILAIRE, *Histoire générale et particulière des anomalies*, Bruxelles, 1837, tome i., p. 376.

Fig. 50. A.

Figure 50. *Diagrammatic Representation of the Genito-Urinary System.*—A, embryonic condition, in which there is no distinction of sex; B, female form; C, male form. The dotted lines in B and C represent the situations which the male and female genital organs assume after the descent of the ovaries and testicles. The small letters in B and C correspond to the capital letters in A.[1]

Fig. 50, A.—A, kidney; B, ureter; C, bladder; D, urachus, developed into the median ligament of the bladder; E, constriction which becomes the urethra; F′, Wolffian body; G, Wolffian duct, with its opening below, G′; H, duct of Müller, united below, from the two sides, into a single tube, J, which presents a single opening, J′, between the openings of the Wolffian ducts; K, ovary or testicle; L, gubernaculum testis or round ligament of the uterus; M, genito-urinary sinus; N, O, external genitalia.

Fig. 50, B (female).—a, kidney; b, ureter; c, bladder; d, urachus; e, urethra; f, remains of the Wolffian body (parovarium); g, remnant of the Wolffian duct; h, Fallopian tube; i, uterus; i′, vagina; k, ovary; l, round ligament of the uterus; m, extremity of the urethra; n, clitoris; n′, corpus cavernosum of the clitoris; n″, bulb of the vestibule; o, external genital opening; p, excretory duct of the gland of Bartholinus.

Fig. 50, C (male).—a, kidney; b, ureter; c, bladder; d, urachus; e, m, urethra; f, epididymis; g, vas deferens; g′, seminal vesicle; g″, ejaculatory duct; h, i, remains of the duct of Müller; k, testicle; l, gubernaculum testis; n, n′, n″, urethra and penis; o, scrotum; p, gland of Cowper; q, prostate.

External Organs of Generation.—The external organs of generation begin to be developed at about the fifth week. At the inferior extremity of the body of the embryon, a small,

[1] HENLE, *Handbuch der systematischen Anatomie des Menschen*, Braunschweig, 1866, Bd. ii., S. 340.

ovoid eminence appears in the median line, at the lower portion of which there is a longitudinal slit, which forms the common opening of the anus and the genital and urinary passages. This is the cloaca. There is soon developed, internally, a septum, which separates the rectum from the vagina, the urethra of the female opening above. In the male, this septum is developed between the rectum and the urethra, the generative and the urinary passages opening together. From this median prominence, two lateral, rounded bodies make their appearance. These are developed, with the median elevation, into the glans penis and corpora cavernosa of the male, or the clitoris and the labia minora of the female. In the male, these two lateral prominences unite in the median line and enclose the spongy portion of the urethra. When there is a want of union of the cavernous bodies in the male, we have the malformation known as hypospadias. In the female, there is no union in the median line, and an opening remains between the two labia minora. The scrotum in the male is analogous to the labia majora of the female; the distinction being that the two sides of the scrotum unite in the median line, while the labia majora remain permanently separated. This analogy is farther illustrated by the anatomy of inguinal hernia, in which the intestine descends into the labia, in the female, and into the scrotum, in the male. It sometimes occurs, also, that the ovaries descend, very much as the testicles pass down in the male, and pass through the external abdominal ring.

From the above description, it is easy to imagine how malformation and malposition of the genital organs may occur, so that it is difficult to determine the sex of the individual. We may have, in a male, absence of beard and a certain degree of development of the mammary glands, with a pelvic conformation approximating, more or less, that of the female; and, on the other hand, a female may have a beard, slight mammary development, and a general conformation of the body resembling that of the male. This may be associated

with corresponding malformations of the genital organs. We may, for example, have a large development of the clitoris, descent of the ovaries, more or less complete occlusion of the vagina, and union of the labia majora, so that it is difficult to determine the sex from an external examination; and opposite vices of formation may occur in the male, the testicles remaining in the pelvic cavity. It is not surprising, therefore, that beings have existed of undetermined sex, and many cases of this kind are on record. In a recent article by Laugier, under the head of "*hermaphrodisme bisexuel*," two cases are quoted in which, apparently, the two sexes were combined. The first case was presented to the Medical Society of Vienna, by Rokitansky, in 1869. This case presented, on post-mortem examination, two ovaries with their Fallopian tubes, a rudimentary uterus, a testicle, and a vas deferens containing spermatozoids. This individual menstruated, had an imperfect penis and a bifid scrotum. The sexual indifference was absolute. The second case was published by Heppner, in 1872. This was a child, six weeks old, which had been preserved in alcohol for several years. It presented ovaries, Fallopian tubes, a uterus, and a vagina opening into the urethra. There were also two bodies which were shown, on microscopical examination, to be testicles, a penis with hypospadia, and a prostate; but there were neither vesiculæ seminales nor vasa deferentia.[1]

Development of the Circulatory System.

The blood and the blood-vessels are developed very early in the life of the ovum, and make their appearance nearly as soon as the primitive trace. The mode of development of

[1] Laugier, *Nouveau dictionnaire de médecine, etc.*, Paris, 1873, tome xvii., p. 505, Article, *Hermaphrodisme.*

Owing to errors in the references given by Laugier, we have not been able to consult the original reports of the two cases quoted above. It is unfortunate that no mention is made of Graafian follicles, in the case quoted from Rokitansky, and that the details of the case quoted from Heppner are so incomplete.

the first vessels differs from that of vessels formed later, as they appear *de novo* in the blastodermic layers, while afterward, vessels are formed as prolongations of preëxisting tubes. Soon after the external and the internal blastodermic membranes have become separated from each other, and the intermediate membrane has been formed at the thickened portion of the ovum which is destined to be developed into the embryon, certain of the blastodermic cells undergo a transformation into blood-corpuscles. These are larger than the blood-corpuscles of the adult, and are generally nucleated.[1] At about the same time, it may be before or after the appearance of the corpuscles, for this point is undetermined, certain of the blastodermic cells fuse with each other and arrange themselves so as to form vessels. Leucocytes are probably developed in the same way as the red corpuscles. The vessels thus formed constitute the area vasculosa, which is the beginning of what is known as the first circulation.

It is evident that the relations of the embryon at different stages of development must require certain variations in the arrangement of the circulatory system. The ovum has, of course, no vascular connection with the mother before the formation of the allantois; it has undergone, however, a certain degree of development, and presents a circulatory system, which extends over the umbilical vesicle. This stage of development of the vascular system constitutes what is known as the first circulation. As the allantois is developed, the circulation over the umbilical vesicle becomes unimportant, and its vessels disappear. Vessels then extend into the allantois, are finally developed into the fœtal portion of the placenta, and what is known as the second circulation is established. This circulation continues throughout intra-uterine life, and, as we know, the embryon and fœtus depend entirely upon the placenta for materials for respiration, nutrition, and growth. At birth, the requirements are

[1] For the differences between the blood-corpuscles of the embryon and the adult, see vol. i., Circulation, p. 119.

again changed. The placental circulation is then abolished, and the arrangement of vessels peculiar to it disappears. Now, for the first time, the pulmonary circulation becomes important. All the blood passes through the lungs before it is sent to the general system, the two sides of the heart become completely separated from each other, and the third, the pulmonary, or adult circulation, is established.

The First, or Vitelline Circulation.—In the development of oviparous animals, the first, or vitelline circulation is very important; for, by these vessels, the contents of the nutritive yolk are taken up and carried to the embryon, constituting the only source of material for its nutrition and growth. In mammals, however, nutritive matter is absorbed almost exclusively from the mother, by simple endosmosis before the placental circulation is established, and by the placental vessels, at a later period. The vitelline circulation is therefore not important, and the vessels disappear with the atrophy of the umbilical vesicle.

The area vasculosa, in mammals, consists of vessels coming from the body of the embryon, forming a nearly circular plexus in the substance of the vitellus, around the embryon. The vessels of this plexus open into a sinus at the border of the area, called the sinus terminalis. It is probable that these vessels are developed *de novo* in the intermediate blastodermic layer, and are not preceded by a distinct membrane; but such a membrane has been described under the name of the vascular blastodermic layer.[1]

If we examine the ovum when the area vasculosa is first formed, we see the embryon lying in the direction of the diameter of the nearly circular plexus of blood-vessels. The plexus surrounds the embryon, except at the cephalic extremity, where the terminal sinuses of the two sides curve downward toward the head, to empty into the omphalo-mesenteric veins. As the umbilical vesicle is separated from

[1] BURDACH, *Traité de physiologie*, Paris, 1838, tome iii., p. 502, *et seq.*

the body of the embryon, it carries the plexus of vessels of the area vasculosa with it, the vessels of communication with the embryon being the omphalo-mesenteric arteries and veins. As these processes are going on, the great central vessel of the embryon becomes enlarged and twisted upon itself, at a point just below the cephalic enlargement of the embryon, between the inferior extremity of the pharynx and the superior *cul-de-sac* of the intestinal canal. The excavation which receives this vessel is called the fovea cardiaca. The different stages of development of the heart, which is formed of the twisted portion of the central vessel, will be described farther on. Simple, undulatory movements take place in the heart of the chick at about the middle of the second day; but there is not, at that time, any regular circulation. At the end of the second day or the beginning of the third, the currents of the circulation are established.[1] The time of the first appearance of the circulation in the human embryon has not been accurately determined.

In the arrangement of the vessels for the first circulation of the embryon, the heart is situated exactly in the median line, and gives off two arches which curve to either side and unite into a single central trunk at the spinal column below. These are the two aortæ, and the single trunk formed by their union becomes the abdominal aorta. The two aortic arches, one of which only is permanent, are sometimes called the inferior vertebral arteries. These vessels give off numerous branches, which pass into the area vasculosa. Two of these branches, however, are larger than the others, pass to the umbilical vesicle, and are called the omphalo-mesenteric arteries. In the embryon of mammals, there are, at first, four omphalo-mesenteric veins, two superior, which are the larger, and two inferior; but, as development advances, the two inferior veins are closed, and we then have two omphalo-mesenteric arteries and two omphalo-mesenteric veins. At about the fortieth day, one artery and one vein

[1] BURDACH, *Traité de physiologie*, Paris, 1838, tome iii., pp. 510, 511.

disappear, and we have then but one omphalo-mesenteric artery and one vein. Soon after, as the circulation becomes established in the allantois, the vessels of the umbilical vesicle and the omphalo-mesenteric vessels are obliterated, and the first circulation is superseded by the second.

As the septum between the two ventricles makes its appearance, that division of the right aortic arch which constitutes the vascular portion of one of the branchial arches disappears and loses its connection with the abdominal aorta; a branch, however, persists during the whole of intra-uterine life, and constitutes the ductus arteriosus; and another branch is permanent, forming the pulmonary artery.

The Second, or Placental Circulation.—As the omphalo-mesenteric vessels disappear, and as the allantois is developed to form the chorion, two vessels, the hypogastric arteries, are given off, first from the abdominal aorta; but afterward, as the vessels going to the lower extremities are developed, the branching of the abdominal aorta is such that the vessels become connected with the internal iliac arteries. The hypogastric arteries pass to the chorion through the umbilical cord, and constitute the two umbilical arteries. At first, there are two umbilical veins; but one of them afterward disappears, and there is finally but one vein in the umbilical cord. It is in this way, the umbilical arteries carrying the blood to the tufts of the fœtal placenta, which is returned by the umbilical vein, that the placental circulation is established.

Corresponding to the four visceral arches, which we have described in connection with the development of the face,[1] are four vascular arches. One of these disappears, and the remaining three undergo certain changes, by which they are converted into the vessels going to the head and the superior extremities. The anterior arches on the two sides are converted into the carotids and subclavians; the second, on the left side, is converted into the permanent aorta, and the

[1] See page 411.

right is obliterated; the third, on either side, is converted into the right and left pulmonary arteries. In the early stages of the development of the vascular system of mammals, the conditions have been compared to the permanent arrangement of the circulatory system in fishes. The heart of fishes remains single; and the heart of mammals is at first single, but afterward becomes divided, by the development of the intra-ventricular septum. The branchial arches in fishes are permanent, receive all the blood from the aortic bulb, and the blood from these arches then passes into the dorsal aorta. This is very nearly the condition of the vascular system when the branchial arches first appear in the embryon of mammals.

FIG. 51.

Transformation of the system of aortic arches into permanent arterial trunks, in the mammalia, after Von Baer.—B, aortic bulb; 1, 2, 3, 4, 5, on each side, the five pairs of aortic arches;[1] 5, the earliest in their appearance; 1, the most recent; *c*, *c*, the two carotids, still united, which are separated at a later period; *s*, *s*, the two subclavians, the right arising from the arteria innominata; *a*, *a*, the aorta; *p*, *p*, the pulmonary arteries; *ca*, the left arterial canal, which is finally obliterated; *cd*, the ductus arteriosus. (LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 984.)

The changes of the branchial arches which we have described are illustrated in the diagrammatic Fig. 51. In this figure, the three branchial arches that remain and participate in the development of the upper portion of the vascular system are 1, 2, 3. The two anterior (3) become the carotids (*c*) and the subclavians (*s*). The second (2) is obliterated on the right side, and becomes the arch of the aorta on the left side. The third (1), counting from above downward, is converted into the pulmonary arteries of the two sides. Upon the left side, there is a large anastomosing vessel (*ca*), between the pulmonary artery of that side and the arch of the aorta, which is the ductus arteriosus. The anastomosing vessel (*cd*) between the right pulmonary artery and the aorta, is obliterated.

[1] Von Baer described five arches, while we have adopted but four. Only three of these arches, however, remain to be developed into permanent vessels.

The mode of development of the veins is very simple. Two venous trunks make their appearance by the sides of the spinal column, which are called the cardinal veins, and run parallel with the superior vertebral arteries, or the two aortæ, emptying finally into the auricular portion of the heart by two canals, which are called the canals of Cuvier. These veins change their relations and connections as the first circulation is replaced by the second. The omphalo-mesenteric vein opens into the heart between the two canals of Cuvier. As development advances, the liver is formed in the course of this vessel, a short distance below the heart, and the vein ramifies in its substance; so that the blood of the omphalo-mesenteric vein passes through the liver before it gets to the heart. We have seen that the omphalo-mesenteric vein is obliterated as the umbilical vein makes its appearance. The blood from the umbilical vein is at first emptied directly into the heart; but this vessel soon establishes the same relations with the liver as the omphalo-mesenteric vein, and its blood passes through the liver before it reaches the central organ of the circulation. As the omphalo-mesenteric vein atrophies, the mesenteric vein, bringing the blood from the intestinal canal, is developed, and this penetrates the liver, becoming, finally, the portal vein.

As the lower extremities are developed, the inferior vena cava makes its appearance between the two inferior cardinal veins. This vessel receives an anastomosing branch from the umbilical vein, before it penetrates the liver, and this branch is the ductus venosus. As the inferior vena cava increases in size, it communicates below with the two inferior cardinal veins; and that portion of the two inferior cardinal veins which remains constitutes the two iliac veins. The inferior cardinal veins, between that portion which forms the iliac veins and the heart, finally become the right and the left azygos veins.

The right canal of Cuvier, as the upper extremities are developed, enlarges and becomes the vena cava descendens, re-

ceiving, finally, all the blood from the head and the superior extremities. The left canal of Cuvier undergoes atrophy, and finally disappears. The upper portion of the superior cardinal veins is developed into the jugulars and subclavians on the two sides. As the lower portion of the left cardinal vein and the left canal of Cuvier atrophy, a venous trunk appears, connecting the left subclavian with the right canal of Cuvier. This increases in size and becomes the left vena innominata, which connects the left subclavian and internal jugular with the vena cava descendens.

Development of the Heart.—The central enlargement of the vascular system in the first circulation, which becomes the heart, is twisted upon itself by a single turn. The portion connected with the cephalic extremity of the embryon gives origin to the arterial system, and the portion connected with the caudal extremity receives the blood from the venous system. The walls of the arterial portion of the heart soon become thickened, while the walls of the venous portion remain comparatively thin. There then appears a constriction, which partly separates the auricular from the ventricular portion. At a certain period of development, the heart presents a single auricle and a single ventricle.

The division of the heart into two ventricles appears before the two auricles are separated. This is effected by a septum, which gradually extends from the apex of the heart upward toward the auricular portion. At the seventh week, there is a large opening between the two ventricles. This gradually closes from below upward, the heart becomes more pointed, and the separation of the two ventricles is complete at about the end of the second month.[1]

At about the end of the second month, a septum begins to be formed between the auricles. This extends from the base of the heart toward the ventricles, but leaves an opening between the two sides, the foramen ovale, or the foramen

[1] BURDACH, *Traité de physiologie*, Paris, 1838, tome iii., p. 514.

of Botal, which persists during the whole of fœtal life. At the anterior edge of the opening of the vena cava ascendens into the right auricle, there is a membranous fold, which projects into the auricle. This is the valve of Eustachius, and it divides the right auricle incompletely into two portions.

During the sixth week, the heart is vertical and situated in the median line, with the aorta arising from the centre of its base. At the end of the second month, it is raised up by the development of the liver, and its point presents forward. During the fourth month, it is twisted slightly upon its axis, and the point presents to the left. At this time, the auricular portion is larger than the ventricles; but the auricles diminish in their relative capacity during the latter half of intra-uterine life. The pericardium makes its appearance during the ninth week.[1]

Early in intra-uterine life, the relative size of the heart is very great. At the second month, its weight, in proportion to the weight of the body, is 1 to 50. This proportion, however, gradually diminishes until, at birth, the ratio is 1 to 120. The proportionate weight in the adult is about 1 to 160.[2] During about the first half of intra-uterine life, the thickness of the two ventricles is nearly the same; but, after that time, the relative thickness of the left ventricle gradually increases.

Peculiarities of the Fœtal Circulation.—In studying the complete course of the blood in the fœtus, which constitutes the second, or the placental circulation, we note peculiarities in two portions of the circulatory system. In the one, a peculiar arrangement is necessitated by the passage of blood to and from the placenta; and in the other, the character of the blood coming from the placenta necessitates a peculiar arrangement of the heart and the great vessels.

The branches from the internal iliac arteries, which pass

[1] BURDACH, *Traité de physiologie*, Paris, 1838, tome iii., p. 515.
[2] QUAIN, *Elements of Anatomy*, London, 1867, vol. i., p. 327.

to the fœtal tufts of the placenta, do not exist in the adult. The ductus venosus, which conveys a portion of the blood of the umbilical vein to the vena cava ascendens, and the umbilical vein itself do not exist in the adult.

The Eustachian valve, situated at the inner margin of the vena cava ascendens as it opens into the right auricle, does not exist in the adult. The foramen ovale, or the opening between the right and the left auricle, through which the blood from the vena cava ascendens is directed into the left auricle, does not exist in the adult. The ductus arteriosus, which conveys the blood from the left pulmonary artery to the arch of the aorta, does not exist in the adult. In the adult, the pulmonary arteries receive all the blood from the right ventricle. In the fœtus, the pulmonary arteries receive a small quantity of blood, as compared with that which passes to the aorta through the ductus arteriosus.

Keeping in view these peculiarities of the circulatory apparatus, the entire course of the blood, during fœtal life, is as follows:

Beginning with the abdominal aorta, we follow the course of blood into the two primitive iliacs, and thence into the internal iliacs. From the two internal iliacs, the two hypogastric arteries arise, which ascend along the sides of the bladder to its fundus, thence pass to the umbilicus, and go to the placenta, forming the two umbilical arteries. In this way, the blood of the fœtus goes to the placenta.

The umbilical vein enters the body of the fœtus at the umbilicus; passes along the margin of the suspensory ligament to the under surface of the liver; gives off one branch of large size, and one or two smaller branches to the left lobe; a branch each to the lobus quadratus and the lobus Spigelii; and the vessel reaches the transverse fissure. At the transverse fissure, it divides into two branches, the larger of which joins the portal vein and enters the liver; and the smaller, which is the ductus venosus, passes to the vena cava ascendens, at the point where it receives the left hepatic vein. Thus, the

greater part of the blood returned to the fœtus from the placenta passes through the liver, a relatively small quantity being emptied into the vena cava by the ductus venosus.

The vena cava ascendens, containing the placental blood which has passed through the liver, the blood conveyed directly from the umbilical vein by the ductus venosus, and the blood from the lower extremities, passes to the right auricle. As the blood enters the right auricle, it is directed by the Eustachian valve, passing behind the valve, through the foramen ovale, into the left auricle. At the same time, the blood from the head and the superior extremities passes down, by the vena cava descendens, in front of the Eustachian valve, through the right auricle, into the right ventricle. The arrangement of the Eustachian valve is such, that the right auricle simply affords a passage for the two currents of blood; the one, from the vena cava ascendens, through the foramen ovale, passes into the left auricle and the left ventricle; and the other, from the vena cava descendens, passes through the right auriculo-ventricular opening, into the right ventricle. It is probable, indeed, that there is very little admixture of these two currents of blood in the natural course of the fœtal circulation. Reid injected the vena cava ascendens with red, and the vena cava descendens with yellow, in a fœtus of seven months, and found very little mixture of the two colors in the passage of the injected material through the right auricle.[1]

The blood poured into the left auricle from the vena cava ascendens through the foramen ovale passes from the left auricle into the left ventricle. The left auricle and the left ventricle also receive a small quantity of blood from the lungs, by the pulmonary veins. Thus the left ventricle is filled. At the same time, the right ventricle is filled with blood which has passed through the right auricle, in front of

[1] Reid, *Injections of the Vessels of the Fœtus, to show some of the Peculiarities of its Circulation.—Physiological Anatomical and Pathological Researches*, Edinburgh, 1848, p. 339.

the Eustachian valve. The two ventricles, thus distended, then contract simultaneously. The blood from the right ventricle passes in small quantity to the lungs, the greater part passing through the ductus arteriosus into the descending portion of the arch of the aorta. This duct is short, half an inch in length, and about the size of a goose-quill. The blood from the left ventricle passes into the aorta and goes to the system. The vessels of the head and superior extremities being given off from the aorta before it receives the blood from the ductus arteriosus, these parts receive almost the pure blood from the vena cava ascendens, the only mixture with the placental blood being the blood from the lower extremities, the blood from the portal system, and the small amount of blood received from the lungs. After the aorta has received the blood from the ductus arteriosus, however, it is mixed blood; and it is this which supplies the trunk and lower extremities. This is one of the reasons assigned by physiologists for the greater relative development of the upper parts of the fœtus.

In Fig. 52, which is partly diagrammatic, the fœtal circulation is illustrated. In endeavoring, in this figure, to give a clear idea of the second circulation, we have not attempted to preserve the exact relations or the relative size of the organs. We have endeavored to represent, by dotted lines, the Eustachian valve, the foramen ovale, and the two auriculo-ventricular orifices. The liver, which is smaller in the diagram than it really is, and the bladder are represented by dotted lines.

There can be no doubt that the fœtus derives materials for its nutrition and growth from the placenta, and that this also serves as a respiratory organ. In another volume,[1] under the head of respiration before birth, we have stated that "Legallois frequently observed a bright-red color in the blood of the umbilical vein; and, on alternately compressing and releasing the vessel, he saw the blood change in color succes-

[1] See vol. i., Respiration, p. 487.

FIG. 59.

L. Subclavian.
Left Carotid.
Art. Innom.
Vena Cava Desc

Art.
le.
Vent.
Right Auric.

Hepatic

Branches
Umbilical
to the Liv

Bladde

Internal Iliac Arteries.

Diagram of the fœtal circulation.

sively from red to dark and from dark to red." This difference in color between the blood of the umbilical arteries and of the umbilical vein has, however, been denied by some authors, who state that all of the fœtal blood, while it is of nearly a uniform color, is lighter than the venous blood of the adult;[1] but Dalton, in a direct observation upon a cat, "nearly arrived at the term of pregnancy," noted that "the difference in color between the umbilical arteries and veins was very distinct. They were both dark, but the color of the veins was very decidedly more ruddy than that of the arteries; *i. e.*, the blood in the umbilical arteries was of the color of the ordinary venous blood, while that of the umbilical veins had a color midway between the ordinary venous and arterial hues. All the fœtuses were healthy, and moved briskly after being taken out of the uterus."[2]

There are numerous observations showing that the fœtus *in utero* makes respiratory efforts when the umbilical vessels are compressed.[3] We believe that these, as well as the first respiration after birth, are due to a want of oxygen in the general system of the fœtus, and think that we have demonstrated this fact by experiments. This point has already been elaborately discussed in another volume.[4] If our experiments and the deductions drawn from them be correct, there can be no doubt with regard to the respiratory function of the placenta, although, as far as we know, there has never been an accurate comparison of the gases contained in the blood of the umbilical arteries and the umbilical vein.

The Third, or Adult Circulation.—When the child is born, the placental circulation is suddenly arrested. After a

[1] ROBIN, *Leçons sur les humeurs*, Paris, 1867, p. 116.

[2] DALTON, *The Physiology of the Circulation.—American Medical Monthly*, New York, November, 1860, p. 340.

[3] B. S. SCHULTZE, *Der Scheintod Neugeborener*, Jena, 1871, S. 64, *et seq.* This is a very elaborate memoir, in which numerous references to experiments are given.

[4] See vol. i., Respiration, p. 479, *et seq.*

short time, the sense of want of air becomes sufficiently intense to give rise to an inspiratory effort, and the first inspiration is made. The pulmonary organs are then, for the first time, distended with air, the pulmonary arteries carry the greatest part of the blood from the right ventricle to the lungs, and a new circulation is established. During the later periods of fœtal life, the heart is gradually prepared for the new currents of blood. The foramen ovale, which is largest at the sixth month, after that time, is partly occluded by the gradual growth of a valve, which extends from below upward and from behind forward, upon the side of the left auricle. The Eustachian valve, which is also largest at the sixth month, gradually atrophies after this time, and, at full term, has nearly disappeared. At birth, then, the Eustachian valve is practically absent; and, after pulmonary respiration becomes established, the foramen ovale has nearly closed. The arrangement of the valve of the foramen ovale is such, that, at birth, a small quantity of blood may pass from the right to the left auricle, but none can pass in the opposite direction. The situation of the Eustachian valve, on the right side of the inter-auricular septum, is marked by an oval depression, called the fossa ovalis.

As a congenital malformation, the foramen ovale may remain open, producing the condition known as cyanosis neonatorum. This may continue into adult life, and is then attended with more or less disturbance of respiration and difficulty in maintaining the normal heat of the body. Usually, the foramen ovale is completely closed at about the tenth day after birth. The ductus arteriosus begins to contract at birth, and is occluded, being reduced to the condition of an impervious cord, at from the third to the tenth day.

When the placental circulation is arrested at birth, the hypogastric arteries, the umbilical vein, and the ductus venosus contract, and they become impervious at from the second to the fourth day. The hypogastric arteries remain pervious at their lower portion, and constitute the superior vesical

arteries. A rounded cord, which is the remnant of the umbilical vein, forms the round ligament of the liver. A slender cord, the remnant of the ductus venosus, is lodged in a fissure of the liver, called the fissure of the ductus venosus.

A history of the development of the various tissues of the body belongs really to general anatomy, and is usually given in works specially devoted to that subject. We have only treated of it incidentally, in our account of the development of the various organs and systems.

CHAPTER XIX.

FŒTAL LIFE—DEVELOPMENT AFTER BIRTH—DEATH.

Enlargement of the uterus in pregnancy—Duration of pregnancy—Size, weight, and position of the fœtus—The fœtus at different stages of intra-uterine life—Multiple pregnancy—Cause of the first contractions of the uterus in normal parturition—Involution of the uterus—Meconium—Dextral pre-eminence—Development after birth—Ages—Death—Cadaveric rigidity—Putrefaction.

As the development of the ovum advances, the uterus is enlarged and its walls are thickened. The form of the organ, also, gradually changes, as well as its position. Immediately after birth, its weight is about a pound and a half, while the virgin uterus weighs less than two ounces. It is a remarkable fact, demonstrated upon the living subject, by Prof. I. E. Taylor, of New York, that the neck of the uterus, while it becomes softer and more patulous during pregnancy, does not change its length, even in the very latest stages of utero-gestation.[1] This fact is in opposition to the statements of

[1] TAYLOR, *On the Non-shortening of the Supra and Infra-Vaginal Portion of the Cervix Uteri up to the End of Pregnancy.—American Medical Times*, New York, 1862, vol. iv., p. 342, *et seq.*

The opinions of obstetricians with regard to the condition of the cervix uteri at the later periods of pregnancy, anterior to the observations of Prof. Taylor, were based chiefly upon digital examinations, which are very deceptive. Dr. Taylor's observations, which are entirely conclusive, were made both with the touch and the speculum. In 1860, Prof. Dalton stated, as the result of post-mortem examinations, "that neither the os internum nor os externum disappeared at all, even up to the end of the ninth month." (*Proceedings of the New York Pathological Society.—New York Journal of Medicine*, 1860, Third Series, vol. viii., p. 258.) A very elaborate historical review of the subject, referring particularly to the views advanced by Stoltz, about the year 1826, and to the opinions of the older writers, is given by Dr. Matthews Duncan, in his *Researches in Obstetrics*, New York, 1868, p. 248, *et seq.*

most obstetricians, who believe that the os internum dilates, and that the neck is gradually absorbed, as it were, by the body of the uterus, during the later months of pregnancy.

We have already studied the remarkable changes which take place in the mucous membrane of the uterus during pregnancy and the mode of formation of the decidua, and we have seen that the mucous membrane of the neck does not participate in these changes and is not thrown off in parturition. The only change, indeed, which we note in the neck, aside from the softening of its texture, is the secretion of the plug of mucus which closes the os.

The changes in the walls of the uterus during pregnancy are very important. The blood-vessels become much enlarged, and the muscular fibres increase immensely in size, so that their contractions are very powerful when the fœtus is expelled.

It is evident that, on account of the progressive increase in the size of the uterus during pregnancy, it cannot remain in the cavity of the pelvis at the later months. During the first three months, however, when it is not too large for the pelvis, it sinks back into the hollow of the sacrum, the fundus being directed somewhat backward, with the neck presenting downward, forward, and a little to the left. After this time, however, the increased size of the organ causes it to extend into the abdominal cavity, so that its fundus eventually reaches the epigastric region. Its axis then has the general direction of the axis of the superior strait of the pelvis.

The enlargement of the uterus and the necessity of carrying on a greatly-increased circulation in its walls during pregnancy are attended with a temporary hypertrophy of the heart. According to Robin, it is mainly the left ventricle which is thickened during utero-gestation, and the increase in the weight of the heart at full term amounts to more than one-fifth.[1] After delivery, the weight of the heart soon returns to nearly the normal standard.

[1] LITTRÉ ET ROBIN, *Dictionnaire de médecine*, Paris, 1878, Article, *Cœur*.

Duration of Pregnancy.—The duration of pregnancy, dating from a fruitful intercourse, must be considered as variable, within certain limits. The method of calculation most in use by obstetricians is, to date from the end of the last menstrual period. Dr. Matthews Duncan, who has made quite a number of observations upon this point, states that the 278th day after the end of the last menses is the average day of delivery; but he admits that his method of calculation is rough, though he cannot find any that is more reliable. The observations upon which this opinion is based are the following: The day was predicted in 153 cases; in 10 cases, confinement occurred on the exact day; in 80 cases, the confinement occurred sooner, presenting an average of 7 days for each case; and, in 63 cases, the confinement occurred later, presenting an average of 8 days for each case.[1] The great difficulty in predicting the exact time of confinement, which is very important in practice, is mainly due to the comparatively small number of reliable observations in which the pregnancy can be dated from a single intercourse, or intercourse occurring within two or three days. We have received from Prof. Fordyce Barker the following very interesting account of a case in which this observation was made, in his own practice: A lady concerning whom there could be no suspicion of inaccuracy, residing in New York, received a visit from her husband, after a long interval of absence. He arrived in this city from New Orleans, remained thirty-six hours, and then went to Europe, where he remained for four months. Exactly 298 days from the date of the first visit of the husband, the lady was confined and delivered by Prof. Barker. This occurred in 1852.[2] Taking into account the various cases which are quoted by authors, in which conception has been supposed to follow a single coitus, there appears to be a range of variation in the duration of pregnancy, according

[1] J. MATTHEWS DUNCAN, *Fecundity, Fertility, Sterility and Allied Topics*, New York, 1871, p. 449.

[2] Communication from Prof. Barker.

to Leishman, of no less than 40 days, the extremes being 260 and 300 days.[1]

In the very interesting observations of Kundrat and Engelmann, on the changes of the uterine mucous membrane during menstruation, to which we have already referred,[2] the idea is advanced that pregnancy dates really from a menstrual period which is prevented, as far as a discharge of blood is concerned, by fecundation of an ovum, and not from the period immediately preceding, in which the flow takes place.[3] If we adopt this view, the changes in the mucous membrane of the uterus ordinarily terminate in a fatty degeneration of the vascular walls, which results in a capillary hæmorrhage; if, however, an ovum be fecundated, these changes do not pass into fatty degeneration, but advance to an hypertrophy, which is the first stage in the formation of the decidua. This view was advanced, a short time before the publication of the researches of Kundrat and Engelmann, by Loewenhardt, in a very elaborate clinical memoir upon the duration of pregnancy.[4] The arguments in opposition to this method of calculating the duration of pregnancy are the following: The time, with relation to the menstrual flow, at which an ovum is discharged has not been accurately determined; and it is certain that ovulation frequently does not take place until after the flow of blood has been established. This question we have fully considered in a previous chapter.[5] It is probable, also, that intercourse is most liable to be followed by fecundation, when it occurs just after the cessation of a menstrual period, and when the female often presents unusual sexual excitement; but it is true that fecundation may follow intercourse at any time. If we admit that fecundation

[1] Leishman, *System of Midwifery*, Glasgow, 1873, p. 188.

[2] See page 306.

[3] Kundrat und Engelmann, *Untersuchungen über die Uterusschleimhaut.—Medizinische Jahrbücher*, Wien, 1873, S. 143.

[4] Loewenhardt, *Die Berechnung und die Dauer der Schwangerschaft.—Archiv für Gynaekologie*, Berlin, 1872, Bd. iii., S. 456, *et seq.*

[5] See page 293.

dates more nearly from a menstrual period prevented than from the last appearance of the flow, it would be necessary to assume that ovulation usually takes place before the flow, and fecundation would be most liable to follow intercourse occurring at that time; for we could hardly admit that an ovum, fecundated at the cessation of a menstrual period, could remain in the generative passages of the female for two or three weeks, before the mucous membrane of the uterus is prepared for its reception. These facts are so strong, that the view advanced by Loewenhardt, and apparently supported by the researches of Kundrat and Engelmann, cannot yet be adopted without reserve.

As regards the practical applications of calculations of the probable duration of pregnancy in individual cases, we must recognize the fact that the duration is variable. If we date from the end of the last menstrual period, we may adopt the average of 278 days, a little more than nine calendar months. If we adopt the view that pregnancy dates from a menstrual period which has been prevented, the duration of intra-uterine life would be about 250 days.

Size, Weight, and Position of the Fœtus.—The estimates of writers with regard to the size and weight of the embryon and fœtus at different stages of intra-uterine life present very wide variations; still, it is important to have an approximative idea, at least, upon these points, and we shall adopt the figures given by Scanzoni, as presenting fair averages. As the measurements and weights are simply approximative, the slight differences between the German and the English standards are not important. It will be useful, also, to give, as is done by Scanzoni, a review of the general development of the organs at different stages.[1]

At the third week, the embryon is from two to three lines in length. This is about the earliest period at which measurements have been taken in the normal state.

[1] Scanzoni, *Lehrbuch der Geburtshilfe*, Wien, 1867, Bd. i., S. 89, *et seq.*

At the seventh week, the embryon measures about nine lines. Points of ossification have appeared in the clavicle and the lower jaw; the Wolffian bodies are large; the pedicle of the umbilical vesicle is very much reduced in size; the internal organs of generation have just appeared; the liver is of large size; the lungs present several lobules.

At the eighth week, the embryon is from ten to fifteen lines in length. The lungs begin to receive a small quantity of blood from the pulmonary arteries; the external organs of generation have appeared, but it is difficult to determine the sex; the abdominal walls have closed over in front.

At the third month, the embryon is from two to two and a half inches long, and weighs about one ounce. The amniotic fluid is then more abundant, in proportion to the size of the embryon, than at any other period. The umbilical cord begins to be twisted; the various glandular organs of the abdomen appear; the pupillary membrane is formed; the limitation of the placenta has become distinct. At this time, the upper part of the embryon is relatively much larger than the lower portion.

At the end of the fourth month, the embryon becomes the fœtus. It is then from four to five inches long, and weighs about five ounces. The muscles begin to manifest contractility; the eyes, mouth, and nose are closed; the gall-bladder is just developed; the fontanelles and sutures are wide.

At the fifth month, the fœtus is from nine to twelve inches long, and weighs from five to nine ounces. The hairs begin to appear on the head; the liver begins to secrete bile, and the meconium appears in the intestinal canal; the amnion is in contact with the chorion.

At the sixth month, the fœtus is from eleven to fourteen inches long, and weighs from one and a half to two pounds. If born at this time, life may continue for a few moments; the bones of the head are ossified, but the fontanelles and sutures are still wide; the prepuce has appeared; the testicles have not descended.

At the seventh month, the fœtus is from fourteen to fifteen inches long, and weighs from two to three pounds. The hairs are longer and darker; the pupillary membrane disappears, undergoing atrophy from the centre to the periphery; the relative quantity of the amniotic fluid is diminished, and the fœtus is not so free in the cavity of the uterus; the fœtus is now viable.

At the eighth month, the fœtus is from fifteen to sixteen inches long, and weighs from three to four pounds. The eyelids are opened and the cornea is transparent; the pupillary membrane has disappeared; the left testicle has descended; the umbilicus is at about the middle of the body, the relative size of the lower extremities having increased.

At the ninth month, the fœtus is about seventeen inches long, and weighs from five to six pounds. Both testicles have usually descended, but the tunica vaginalis still communicates with the peritoneal cavity.

At birth, the infant weighs a little more than seven pounds, the usual range being from four to ten pounds, though these limits are sometimes exceeded.

The position of the fœtus, in the great majority of cases, excluding abnormal presentations, is with the head downward; and why this is the usual and the normal position, is a question which has been the subject of much discussion. As we have just seen, in the early stages of pregnancy, the fœtus floats quite freely in the amniotic fluid. Upon this point, Dr. Matthews Duncan has made the following interesting experiments: Securing the limbs of the fœtus in the natural position which it assumes *in utero*, by means of threads, and immersing it in a solution of salt of nearly its own specific gravity, he found that it naturally gravitated to nearly the normal position, with the head downward.[1] It is probable, judging from these observations, that the natural gravitation of the head and of the upper part of the fœtus is the determining cause of the ordinary position *in utero*.

[1] J. Matthews Duncan, *Researches in Obstetrics*, New York, 1868, p. 27.

The shape of the uterus at full term is ovoid, the lower portion being the narrower. The fœtus has the head slightly flexed upon the sternum, the arms flexed upon the chest and crossed, the spinal column curved forward, the thighs flexed upon the abdomen, the legs slightly flexed, and usually crossed in front, and the feet flexed upon the legs, with their inner margin drawn toward the tibia. This is the position in which the fœtus is best adapted to the size of the uterine cavity, and in which the expulsive force of the uterus can be most favorably exerted, both as regards the fœtus and the generative passages of the mother.

Multiple Pregnancy.—It is not very rare to observe two children at a birth, and cases are on record where there have been four and even five, though in these latter instances the children generally survive but a short time, or, as is more common, abortion takes place during the first months. Three at a birth, though rare, has been often observed; and we have in mind at this moment a case of three females, triplets, all of whom lived past middle age.

In cases of twins, it is an interesting question to determine whether the development always takes place from two ova, or whether a single ovum may be developed into two beings. In the majority of cases, twins are of the same sex, though sometimes they are male and female. In some cases, there are two full sets of membranes, each fœtus having its distinct decidua, placenta, and chorion; in others, there is a single chorion and a double amnion; but, in some, both fœtuses are enclosed in the same amnion. As a rule, the two placentæ are distinct; but sometimes there is a vascular communication between them, or what appears to be a single placenta may give origin to two umbilical cords. If there be but a single chorion and amnion and a single placenta, it has been thought that the two beings are developed from a single ovum; otherwise, it would be necessary to assume that there were originally two sets of membranes, which had become

fused into one. The instances on record, one of which we have given,[1] of twins, one white and the other black, show conclusively that two ova may be developed in the uterus at the same time. While there can be no doubt upon this point, the question of the possibility of the development of two beings from a single ovum remains unsettled. It is thought to be more difficult to understand how two conjoined monsters, like the celebrated Siamese twins, who have just died, could be developed from two ova which became fused, than to imagine the development of two beings from a single ovum. This question, however, belongs to teratology, and could only be settled by observations of conjoined monsters very early in their development, which do not exist in literature.

As pathological conditions, we have extra-uterine pregnancies, in which the fecundated ovum, forming its attachments in the Fallopian tube (Fallopian pregnancy) or within the abdominal cavity (abdominal pregnancy), undergoes a certain degree of development. The uterus usually enlarges, in these instances, and forms an imperfect decidua.

Cause of the First Contractions of the Uterus in Normal Parturition.—The cause of the first contraction of the uterus in normal parturition is undoubtedly referable to some change in the attachment of its contents, which causes the fœtus and its membranes to act as a foreign body. When, for any reason, it is advisable to cause the uterus to expel its contents before the full term of pregnancy, the most physiological method of bringing on the contractions of this organ is to cautiously separate a portion of the membranes, as is often done by introducing an elastic catheter between the ovum and the uterine wall. A certain time after this operation, the uterus contracts to expel the ovum, which then acts as a foreign body.

In the normal state, toward the end of pregnancy, the cells of the decidua vera and of that portion of the placenta

[1] See page 348.

which is attached to the uterus undergo fatty degeneration, and, in this way, there is a gradual separation of the outer membrane, so that the contents of the uterus gradually lose their anatomical connection with the mother. When this change has progressed to a certain extent, the uterus begins to contract; each contraction then separates the membranes more and more, the most dependent part pressing upon the os internum, and the subsequent contractions are probably due to reflex action. The first "pain" is induced by the presence of the fœtus and its membranes as a foreign body,[1] a mechanism similar to that which obtains when premature labor has been brought on by separation of the membranes.

We shall not describe the mechanism of parturition, although this is entirely a physiological process, for the reason that it is necessarily considered elaborately in works on obstetrics. The first contractions of the uterus, by pressing the bag of waters against the os internum, gradually dilate the cervix; the membranes usually rupture when the os is pretty fully dilated, and the amniotic fluid is discharged; the head then presses upon the outlet; and, the uterine contractions becoming more and more vigorous and efficient, the child is brought into the world, this being followed by the expulsion of the membranes and placenta. There then follows a tonic contraction of the muscular walls of the uterus, which becomes a hard, globular mass, easily felt through the flaccid abdominal walls. The very contractions of the muscular fibres of the uterus which expel the fœtus close the vessels ruptured by the separation of the placenta and arrest the hæmorrhage from the mother. The changes which then take place in the respiration and the circulation of the infant have been fully considered in connection with the development of the circulatory system.[2]

Involution of the Uterus.—At from four to six days, and

[1] HENNIG, *Studien über den Bau der menschlichen Placenta*, Leipzig, 1872, S. 26.

[2] See page 441.

seldom later than eight days after parturition, the uterus has sensibly advanced in the process of involution; and it is then gradually reduced to the size and structure which it presents during the non-pregnant condition, though it never becomes quite as small as in the virgin state. The new mucous membrane, which has been developing during the latest periods of pregnancy, becomes perfect at about the end of the second month after delivery. It has then united, at the os internum, with the mucous membrane of the neck, which does not participate in the formation of the decidua. The muscular fibres, after parturition, present granules and globules of fat in their substance, and are gradually reduced in size, as the uterus becomes smaller. Their involution is complete at about the end of the second month. During the first month, and particularly within the first two weeks after delivery, there is a sero-sanguinolent discharge from the uterus, which is due to disintegration of the blood and of the remains of the membranes in its cavity, this *débris* being mixed with a certain amount of sero-mucous secretion. This discharge constitutes the lochia, which are at first red, but become paler as they are reduced in quantity, and disappear.

During lactation, which we have already considered in another volume,[1] the processes of ovulation and menstruation are usually arrested, though this is not always the case. In the volume on secretion, we have given a full description of the vernix caseosa, and, in the same volume, we have stated what is known with regard to the properties and composition of the urine of the fœtus.[2]

Meconium.—At about the fifth month, there appears a certain amount of secretion in the intestinal canal, which becomes more abundant, particularly in the large intestine, as development advances. This is rather light-colored or grayish in the upper portion of the small intestine, becoming yel-

[1] See vol. iii., Secretion, p. 72, *et seq.* [2] Ibid., pp. 67, 221.

lowish in the lower portion, and is of a dark-greenish color in the colon. The dark, pasty, adhesive matter, which is discharged from the rectum soon after birth, is called the meconium.

The meconium appears to consist of a thick, mucous secretion, with numerous grayish granules, a few fatty granules, intestinal epithelium, and, frequently, crystals of cholesterine, this occurring, according to Robin and Tardieu, in about two out of five specimens. The color seems to be due to granulations of the coloring matter of the bile.[1] According to Dalton, none of the biliary salts can be detected in the meconium by Pettenkofer's test.[2] The constituent of the meconium which, in our own observations, we have found to possess the greatest physiological importance, is cholesterine. Although but few crystals of cholesterine are found on microscopical examination, the simplest processes for its extraction will reveal the presence of this principle in large quantity. In a specimen of meconium in which we made a quantitative examination, the proportion of cholesterine was 6·245 parts per 1,000. It is a significant fact, that the meconium contains cholesterine and no stercorine, the stercorine, in the adult, resulting from a transformation of cholesterine by the digestive fluids, which are probably not secreted during intra-uterine life.

None of the secretions concerned in digestion appear to be produced *in utero*, and it is also probable that the true biliary salts are not formed at that time; but we know that the processes of disassimilation and excretion are then active, and the cholesterine of the meconium is the product of the excretory action of the liver. The relations of cholesterine as an excrementitious principle have already been very fully discussed.[3]

[1] Robin et Tardieu, *Mémoire sur l'examen microscopique des taches formées par le méconium et l'enduit fœtal*, Paris, 1857, p. 21, *et seq.*

[2] Dalton, *Human Physiology*, Philadelphia, 1871, p. 668.

[3] See vol. iii., Excretion, p. 267, *et seq.*

Dextral Preëminence.—The curious fact, that most persons by preference use the right arm, leg, eye, etc., instead of the left, while, as exceptions, some use the left in preference to the right, has excited a great deal of discussion, even among the earlier writers. There can be no doubt with regard to the fact of a natural dextral preëminence; and, also, that left-handedness is congenital, difficult, if not impossible, to correct entirely, and not due simply to habit. It would appear that there must be some condition of organization, which produces dextral preëminence in the great majority of persons, and left-handedness, as an exception; but what this condition is, it is very difficult to determine. Several years ago, J. Achille Comte proposed the theory that, in the most common position of the fœtus *in utero,* the left side of the body is pressed against the spinal column of the mother, and, as a consequence, the muscles of that side are not so fully developed as upon the right side. To carry out this explanation, it would be necessary to show that, in the position in which the right side is toward the back of the mother, the individual is left-handed. Comte has endeavored to show this, but his cases are not sufficiently numerous and clear to carry conviction.[1] Another explanation, very often offered by anatomists, is, that the right subclavian artery arises nearer the heart than the left, that the right arm is therefore better supplied with arterial blood, develops more fully, and is, consequently, generally used in preference to the left; but we cannot explain the exceptional predominance of the left hand by an inversion of this arrangement of vessels. The idea advanced by Dr. Dwight, of Boston, that "one-half of the brain (the left) has a more acute perception of tactile impressions, while the other (the right) distinguishes more readily different degrees of temperature and weight," is based upon a few observations on these points in right-handed persons and one

[1] J. Achille Comte, *Recherches anatomico-physiologiques, relatives à la prédominance du bras droit sur le bras gauche.—Journal de physiologie,* Paris, 1828, tome viii., p. 41, *et seq.*

on a left-handed person. The data given by Dr. Dwight are not sufficient, however, to render this explanation satisfactory.[1]

The most important anatomical and pathological facts bearing upon the question under consideration are the following: Dr. Boyd has shown that the left side of the brain almost invariably exceeds the right in weight, by about one-eighth of an ounce. In aphasia, the lesion is almost always on the left side of the brain. These facts point to a predominance of the left side of the brain, which presides over the movements of the right side of the body. Again, a few cases of aphasia with left hemiplegia, the lesion being on the right side of the brain, have been reported as occurring in left-handed persons. These points we have noted in treating of the nervous system.[2]

Dr. Ogle, in a recent paper on right-handedness, gives several instances of aphasia in left-handed persons, in which the brain-lesion was on the right side. In two left-handed individuals, the brain was examined and compared with the brain of right-handed persons. It was found that the brain was more complex on the left side in the right-handed, and on the right side in the left-handed.[3] In the discussion which followed the presentation of this paper, Dr. Charlton Bastian stated that he had found the gray matter of the brain to be generally heavier on the left than on the right side.[4] With regard to the cause of the superior development of the left side of the brain, the only explanation offered was the fact

[1] Dwight, *Right and Left Handedness.—Journal of Psychological Medicine*, New York, 1870, vol. iv., p. 539.

[2] See vol. iv., Nervous System, pp. 356, 357.

[3] Ogle, *On Dextral Preëminence.—Medico-Chirurgical Transactions*, London, 1871, vol. liv., p. 279, *et seq.*

In this very interesting paper, Dr. Ogle discusses most of the theories of dextral preëminence, and gives some very curious observations, showing that this condition exists in monkeys and parrots. Most monkeys, he found, used the members of the right side by preference, while a few were distinctly left-handed.

[4] *New York Medical Journal*, 1872, vol. xv., p. 279.

that the arteries going to the left side are usually larger than those on the right. There were no observations with regard to the comparative size of the arteries upon the two sides in left-handed persons.

Reasoning from the facts just stated, Dr. Ogle conceives that dextral preëminence depends upon a natural predominance of the left side of the brain, the reverse obtaining in the left-handed. This view seems to afford the most rational explanation of dextral preëminence. It is generally true that the members on the right side are stronger than the left, particularly the arm; but this is not always the case, even in the right-handed. A not inconsiderable practical experience in athletic exercises has led us to observe that the right hand is more conveniently and easily used than the left, from which fact we derive the term dexterity; but that the left arm is often stronger than the right. In many feats of strength, the left arm appears less powerful than the right, because we have less command over the muscles. As a single illustration of this, we may mention the feat of drawing the body up with one arm, which requires unusual strength, but very little dexterity. In a number of right-handed persons, we find many who perform this feat more easily with the left arm, and not a few who can accomplish it with the left arm and not with the right. When we come to the cause of the superior development of the left side of the brain, we must confess that the anatomical explanation is not entirely satisfactory. We can only say that the two sides of the brain are generally not exactly equal in their development, the left side being usually superior to the right, and that we ordinarily use the muscles of the right side of the body in preference to those on the left side.

Development after Birth, Ages, and Death.

When the child is born, the organs of special sense and the intelligence are dull; there is then very little muscular power; and the new being, for several weeks, does little more than

eat and sleep. The natural food at this time is the milk of the mother, and the digestive fluids do not, for some time, possess the varied solvent properties that we find in the adult, though observations upon the secretions of the infant are few and rather unsatisfactory. The full activity of pulmonary respiration is gradually and slowly established. Young animals appropriate a comparatively small quantity of oxygen, and, just after birth, present a much greater power of resistance to asphyxia than the adult.[1] The power of maintaining the animal temperature is also much less in the newly-born.[2] The process of ossification, development of the teeth, etc., have already been considered.[3] The hairs are shed and replaced by a new growth a short time after birth.[4] The fontanelles gradually diminish in size after birth, and are completely closed at the age of about four years.

The period of life which dates from birth to the age of two years is called infancy. At the age of two years, the transition takes place from infancy to childhood. The child is now able to walk without assistance, the food is more varied, and the digestive operations are more complex. The special senses and the intelligence become more acute, and the being begins to learn how to express ideas in language. The child gradually develops, and the milk-teeth are replaced by the permanent teeth. At puberty, which begins at from the fourteenth to the seventeenth year, a little earlier in the female, the development of the generative organs is attended with important physical and moral changes.

The different ages recognized by the older writers were as follows: Infancy, from birth to the age of five years; adolescence, or youth, to the twenty-fifth year; adult age, to the thirty-fifth year; middle life, to the fiftieth year; old age, to the sixtieth year; and then, extreme old age. A man may be regarded at his maximum of intellectual and physical devel-

[1] See vol. i., Respiration, pp. 420, 490.

[2] See vol. iii., Animal Heat, p. 405.

[3] See pages 393, 416.

[4] KÖLLIKER, *Éléments d'histologie humaine*, Paris, 1868, p. 180.

opment at about the age of thirty-five, and he begins to decline after the sixtieth year, although such a rule, as regards intellectual vigor, would certainly meet with numerous exceptions.

We do not propose to consider, in this connection, the psychological variations which occur at different ages, but, as regards the general process of nutrition, it may be stated, in general terms, that the appropriation of new matter is a little superior to disassimilation up to about the age of twenty-five years; between twenty-five and forty-five, these two processes are nearly equal; and, at a later period, the nutrition does not completely supply the physiological waste of the tissues, the proportion of organic to inorganic matter gradually diminishes, and death follows, as an inevitable consequence of life. In old age, the muscular movements gradually become feeble; the bones contain an excess of inorganic matter; the ligaments become stiff; the special senses are usually obtuse; and there is a diminished capacity for mental labor, with more or less loss of the memory and of intellectual vigor. It is a curious fact that remote events are more clearly and easily recalled to the mind in old age, than those of recent occurrence; and, indeed, early impressions and prejudices then appear to be unusually strong.

It frequently happens, in old age, that some organ essential to life gives way, and that this is the immediate cause of death; or that an old person is stricken down by some disease to which his age renders him peculiarly liable. It is so infrequent to observe a perfectly physiological life, continuing throughout the successive ages of man, that it is almost impossible to present a picture of physiological death; but we sometimes observe a gradual fading away of vitality in old persons, who die without being affected with any special disease. It is also difficult to fix the natural period of human life. Some persons die, apparently of old age, at seventy, and it is rare that life is preserved beyond one hundred years. In treating of the so-called vital point, we

have stated that there does not seem to be any such occurrence, except under conditions of most extraordinary external violence, as instantaneous death of all parts of the organism.[1] If we confine ourselves to physiological facts, we cannot admit the existence of a single vital principle which animates the entire organism. Each tissue appears to have its peculiar property, dependent upon its exact physiological constitution, which we call vitality; a term which really explains nothing. The tissues usually die successively, and not simultaneously, nearly all of them being dependent upon the circulating, oxygen-carrying blood for the maintenance of their physiological properties. It has been demonstrated, indeed, that the so-called vital properties of tissues may be restored, after apparent death, by the injection of blood into their vessels.[2]

After death, there is often a discharge of the contents of the rectum and bladder, and parturition, even, has been known to take place.[3] The appearance which indicates growth of the beard is probably due to shrinking of the skin and, perhaps, contraction of the smooth muscular fibres attached to the hair-follicles. The most important phenomenon, however, which is observed before putrefaction begins, is a general rigidity of the muscular system.

Cadaveric Rigidity.—At a variable period after death, ranging usually from five to seven hours, all of the muscles of the body, involuntary as well as voluntary, become rigid, and can only be stretched by the application of considerable force. Sometimes, especially after long-continued and ex-

[1] See vol. iv., Nervous System, p. 410.

[2] In vol. i., Blood, p. 99, we have cited a curious experiment by Brown-Séquard, in which blood was passed from a living dog into the carotid of a dog just dead from peritonitis. The animal was so far revived as to sustain himself on his feet, wag his tail, etc., and died a second time, twelve and a half hours after. In this experiment, insufflation was employed in addition to the transfusion. In cases of death from hæmorrhage, it is well known that life may be brought back, as it were, by artificial restoration of the blood.

[3] SYMONDS, *Cyclopædia of Anatomy and Physiology*, London, 1835–1836, vol. i., p. 804, Article, *Death*.

hausting diseases, this rigidity appears as soon as a quarter of an hour after death. In the case of persons killed suddenly, while in full health, it may not be developed until twenty or thirty hours after death, and continues for six or seven days.[1] Its average duration is from twenty-four to thirty-six hours; and, as a rule, it is more marked and lasts longer, the later it appears. In warm weather, cadaveric rigidity appears early and continues for a short time. When the contraction is overcome by force, after the rigidity has been completely established and has continued for some time, it does not reappear. The rigidity of the muscular system extends to the muscular coats of the arteries and the lymphatics.[2] It is for this reason that the arterial system is usually found empty after death.[3] The rigidity first appears in the muscles which move the lower jaw; then, according to the observations of Nysten, it is noted in the muscles of the trunk and neck, extends to the arms, and finally, to the legs, disappearing in the same order of succession.[4] The stiffening of the muscles is due to a sort of coagulation of their substance, analogous to the coagulation of the blood, and is probably attended with some shortening of the fibres; at all events, the fingers and thumbs are generally flexed. That the rigidity is not due to coagulation of the blood, is shown by the fact that it occurs in animals killed by hæmorrhage.

According to John Hunter, the blood does not coagulate nor do the muscles become rigid in animals killed by lightning or hunted to death;[5] but it is a question, in these in-

[1] Symonds (*loc. cit.*) observed rigidity in the body of a criminal executed by hanging, eight days after death, but had no opportunity of ascertaining at what time it commenced.

[2] Magendie, *Précis élémentaire de physiologie*, Paris, 1836, tome ii., p. 225.

[3] See vol. i., Phenomena in the Circulatory System after Death, p. 351.

Parry, in his experiments published in 1816, noted contraction in the arteries after death. (Parry, *An Experimental Inquiry into the Nature, Cause, and Varieties of the Arterial Pulse*, London, 1816, pp. 16, 46.)

[4] Nysten, *Recherches de physiologie*, Paris, 1811, p. 386.

[5] Hunter, *Lectures on the Principles of Surgery*, Philadelphia, 1839, p. 35.

stances, whether the rigidity does not begin very soon after death and continue for a brief period, so that it may escape observation. This is the view entertained by Brown-Séquard, who has made numerous experiments on this point.[1] As a rule, rigidity is less marked in very old and in very young persons than in the adult. It occurs in paralyzed muscles, provided they have not undergone extensive fatty degeneration.

Under ordinary conditions of heat and moisture, as the rigidity of the muscular system disappears, the processes of putrefaction commence. The various tissues, with the exception of certain parts, such as the bones and teeth, which contain a large proportion of inorganic matter, gradually decompose, forming water, carbonic acid, ammonia, etc., which pass into the earth and the atmosphere. The products of decomposition of the organism are then in a condition in which they may be appropriated by the vegetable kingdom.

[1] BROWN-SÉQUARD, *Relations entre l'irritabilité musculaire, la rigidité cadavérique et la putréfaction.—Journal de la physiologie*, Paris, 1861, tome iv., p. 271, *et seq.*

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THE END.